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SEASONAL AND LATITUDINAL VARIATIONS IN THE
CIRCADIAN RHYTHMS OF THREE SPECIES OF
SMALL RODENTS IN NORTHERN CANADA

BY



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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Seasonal and latitudinal variations in the circadian rhythms of three species of small rodents in northern Canada" submitted by Lucius LeBaron Stebbins, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The activity of two allopatric species, Clethrionomys gapperi and C. rutilus were studied near their common border at Heart Lake, Northwest Territories, 700 miles north of Edmonton during winter of 1965-1966 in order to test the hypothesis that their circadian rhythms are similar, and therefore increase competition between the species and act as a behavioural barrier to sympatry. The activity of C. gapperi was also studied at Edmonton in the winter and spring of 1964-1965 in an effort to detect latitudinal differences in their circadian rhythms. The activity of P. maniculatus was studied at Heart Lake to determine the effect of torpor on their circadian rhythms. In each species, an effort was made to relate seasonal changes in circadian rhythms to seasonal changes in photoperiod, temperature, and growth and reproduction of natural populations.

In winter activity was measured by recording passages through a door in subnivean cages exposed to nearly normal changes in temperature and light.

Differences in occurrence and duration of daily peaks of activity of C. gapperi and C. rutilus were present in winter and spring at Heart Lake. It was concluded that circadian rhythms probably do not reinforce competition between the species, though the alternative possibility is considered.

The circadian rhythms of C. gapperi at Heart Lake differed at all seasons from those of C. gapperi at Edmonton. It was concluded that the causative factor was probably related to photoperiod, but that

interactions with C. rutilus along the zone of contact might also be important.

The daily peaks of each species were of longer duration and higher amplitude in spring than in winter. The spring increases in activity were attributed primarily to increased energy demands associated with growth and reproduction.

P. maniculatus had extremely low levels of activity in winter. They were frequently observed in torpor though food was plentiful. It was concluded that in this species torpor occurs naturally as an adaptation to conserve energy and increase survival in winter.

In C. gapperi, seasonal changes in the shape of the daily peaks of activity were caused by seasonal changes in the frequency and duration of the short term cycles.

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INTRODUCTION

This study was done to test three hypotheses. The first was that daily patterns of activity of Clethrionomys gapperi and C. rutilus, two allopatric species which meet along a narrow zone of contact at about 60°N. latitude between Hudson's Bay and the Pacific Ocean, are similar, and therefore reinforce competition, which, in the absence of any obvious geographical feature, acts as a behavioural barrier to sympatry.

The second hypothesis was that, at temperature and subarctic latitudes, daily patterns of activity of C. gapperi, C. rutilus, and Peromyscus maniculatus would vary in response to marked seasonal variations in photoperiod, temperature, and levels of illumination.

The third hypothesis was that seasonal changes in level and patterns of activity of the two Clethrionomys spp. would be lower in fall and winter than spring because of behavioural and physiological changes associated with reproduction and a higher rate of growth in spring. A second part of this hypothesis was that in winter P. maniculatus would have a much lower level of activity than Clethrionomys spp. because the activity of deer mice would be reduced by torpor in winter.

Two basic patterns of activity are common among rodents and insectivores so far investigated: (1) a 2 to 5 hour short term or feeding cycle, which consists of short bursts of activity every few hours throughout the day and night, and (2) a 24 hour cycle, often called a circadian rhythm (Elton et al., 1931; Davis, 1933; Calhoun, 1945; Miller, 1955; Mann and Stinson, 1957; Pearson, 1962; Gebczynski, 1964).

The short term rhythm has been reported in a variety of rodents. Some investigators feel it is basically a feeding and digestion cycle

(Richter, 1927; Elton et al. 1931; Chitty and Shorten, 1946; Miller, 1955; and Brown, 1956), while others suggest it is an endogenous rhythm which is independent of food (Munn, 1950; Crowcroft, 1953; Hansen, 1957; Mann and Stinson, 1957; Pearson, 1962; Gebczynski, 1964).

When the short term cycle occurs with no superimposed circadian rhythm, the resulting pattern consists of short bursts of activity spaced evenly throughout the day. This is called a polyphasic pattern.

The 24 hour cycle usually has a nocturnal or a diurnal period in which much of the daily activity is concentrated. This period of high activity is called the daily activity peak. It is often double in appearance, characteristic for a given species, and generally considered to be in phase with some aspect of photoperiod. The relationship of the peak of activity to photoperiod is called the phase of the circadian rhythm. The 24 hour rhythm is quite variable. Differences occur between species, and within species between seasons and environments.

Little is known of the adaptive value of circadian rhythms in rodents, though there is general agreement that they are in synchrony with predator-prey relationships and competition (Hamilton, 1937; Allee et al., 1949; Miller, 1955; Cloudsley-Thompson, 1960; Pearson, 1962; Swade and Pittendrigh, 1967). Prerequisite to further knowledge of the adaptive value of circadian rhythms of rodents is more precise data on seasonal changes in patterns of activity, allowing one to relate these data to seasonal changes in some aspects of the natural history, such as reproduction, growth, nutrition, temperature, and light. In some studies done at high latitudes, seasonal changes of circadian rhythms have been demonstrated. (Erkinaro, 1961; Folk, 1964, 1966; Folk et al., 1966;

Peiponen, 1962; Grodzinski, 1963). There has been little effort to relate these changes to the natural history of the species studied.

Patterns of activity are ecologically important, if not because they directly influence survival and distribution, then because they are influenced by many of the environmental factors which do influence survival and distribution (Johnson, 1926; Park, 1935; Hamilton, 1937; Armstrong, 1954; Miller, 1955; Hansen, 1957; Cloudsley-Thompson, 1960; Pearson, 1962). They may thus serve as indicators of environmental stress, and one might study some aspects of their adaptive significance by correlating variations in activity patterns with certain changes in general biology, or the environment. Food requirements (Elton et al., 1931; Davis, 1933; Wald and Jackson, 1944; Calhoun, 1945; Miller, 1955; Koshkina, 1957; Muul, 1965; Williams, 1959; Grodzinski, 1960), sexual activity (Wald and Jackson, 1944), and temperature (Aschoff, 1960; Bruce, 1960; Bünning, 1964; Gebczynski, 1964; Enright, 1965; Folk, 1966) have been shown to affect the activities of a variety of rodents.

Peromyscus maniculatus, which are reported to spend part of the winter in a state of torpor (Howard, 1949, 1951; Hudson, 1965, 1967) might be favorable to use for research into relationships between activity and the phenology of growth and reproduction of a species. Their level of activity in winter is apparently decreased as a result of torpor. Thus, their winter survival and spring reproductive success might be affected by a conservation of energy resources during winter (Lyman, 1954; Johansen and Krog, 1959; Smith and Criss, 1967; Jameson, 1965). A comparison with Clethrionomys spp., which are not reported to enter torpor during winter, might also be revealing.

With this in mind, I conducted the following studies at Edmonton, Alberta and Heart Lake, Northwest Territories during the winter and spring of 1964 - 1965 and 1965 - 1966; an investigation of daily and seasonal variations in activity of Clethrionomys gapperi at a subarctic and a temperate latitude, an investigation of daily and seasonal variations in activity of C. rutilus and P. maniculatus at a subarctic latitude, and simultaneously, studies of growth and reproduction of the 3 species. I chose to do the studies in winter and spring because changes in the reproductive biology, rate of growth, and patterns of activity of small mammals occur in this period, because the physical components of the environment, photoperiod, level of solar illumination, temperature and snow cover vary markedly between December and June, and because little is known of the winter ecology of small northern rodents.

METHODS AND MATERIALS

Activity patterns of C. gapperi were studied from December, 1964, to June 30, 1965, at Edmonton, Alberta (53°N). The activity patterns of C. gapperi and C. rutilus were studied during December, 1965, and May and June, 1966, at the Heart Lake Biological Station of the University of Alberta (60°, 45'N), 50 miles west of Hay River, Northwest Territories, Canada. The activity patterns of P. maniculatus were studied from December, 1965, to June, 1966, at Heart Lake. Simultaneous studies of growth and reproduction of the natural populations of Clethrionomys and Peromyscus, and recordings of air and ground surface temperatures, photoperiod, levels of solar illumination, and depth of snow cover were made near Edmonton and Heart Lake.

Activity

At Edmonton, the activity patterns of 3 male and 3 female C. gapperi from the Northwest Territories, and 3 male and 3 female C. gapperi from the Edmonton area were studied. Specimens from the Edmonton area were trapped immediately prior to the experiments. The northern C. gapperi were born the previous summer in a colony at Edmonton. The parental stock was captured in June, 1963, near the Heart Lake Biological Station. In late January of 1964, studies of northern C. gapperi were discontinued, as I could not obtain stock to replace those that died. At Heart Lake, 2 males and 2 females of each species of Clethrionomys, and 2 male and 1 female P. maniculatus were studied. These were trapped in October, 1965, and housed in cages in an unheated trailer until the beginning of the experiments.

I used activity cages of $\frac{1}{2}$ inch wire mesh, measuring 30 X 30 X 60 centimeters. These were placed on the forest floor in quiet, natural areas.

Clethrionomys were housed one to a cage and provided with nest boxes 8 X 8 X 16 centimeters which were insulated on all surfaces by 2.5 centimeters of styrofoam. The animals entered the nest boxes through small tunnels in which swinging doors were located. The doors operated mercury switches in adjacent boxes. The switches activated a 20 pen Esterline Angus event recorder in a nearby trailer. All movements in and out of the nest boxes were recorded. Terylene fiber was provided for nesting material. Sunflower seeds and Purina laboratory mouse food were fed ad libitum. Cages and nest boxes were cleaned, and fresh food added, every 2 weeks. In winter, cages were partially or completely filled with snow. The animals had to tunnel to find food or exercise. The only protection from rain was the nest box.

The decision to test P. maniculatus was made after the first winter's trapping results at Edmonton indicated the possibility of winter torpor. In winter, 3 deer mice were placed in one nest box because of the reported facilitation of torpor by huddling. Techniques were the same for deer mice as for Clethrionomys except that during winter their cages were cleaned and the mice fed only once a month. Perhaps because of torpor, their food consumption was low and nest boxes did not become as soiled as those of Clethrionomys.

In late March each deer mouse was placed in a separate activity cage. This was done because it was doubtful that the high level of

spring activity of the 3 mice could be accurately measured by a single recording device.

For analysis, total marks of each group were averaged by hour, and hourly 2 week averages were computed and graphed. A computer program was written to obtain these averages and this program is on file with the Zoology Department at the University of Alberta, along with the chart paper, data sheets, and punch cards.

Trapping

For studies of growth and reproduction, snap-trapping was conducted periodically at both latitudes. Snap-trapping was conducted at 2 week intervals in the period of study at Edmonton. At Heart Lake, samples were taken in early October, 1964, before the advent of the snow cover; mid-April, 1965, just before loss of snow cover; at 2 week intervals in the fall of 1965, spring, 1966; and periodically during the intervening winter.

Trapping methods were identical at both latitudes. In the absence of snow, 2 trap lines, 30 paces apart, were set for 3 nights. Each line had 20 or 40 traps set at intervals of 10 paces. Traps were placed under bushes, or in other likely places and checked mornings. No trap line was used more than once. When snow cover was present, varying numbers of traps were placed in lines at about 30 foot intervals. Traps were placed under thick undergrowth, or other places covered with snow above, but snow free at ground level. Even with a 30 inch snow cover, such places were numerous and could be reached by digging. There were often natural openings or rodent tunnels to the surface at such locations.

At Edmonton, several areas within a 5 mile radius of the activity experiments were trapped. The areas trapped were chosen primarily for the accessibility there being an abundance of aspen forest in the area.

Trapping areas near Heart Lake were less uniform. Preliminary trapping was conducted in several types of habitat to investigate possible inherent differences in population levels. Areas with mature spruce gave the highest trapping returns for all 3 species used in this study. P. maniculatus were also abundant in poplar stands.

All specimens were frozen in double plastic bags (Banks, 1965) for later processing. Total length, length of the tail and hindfoot, weights, and reproductive condition were recorded.

A female was judged to be approaching breeding condition if the vagina was perforate and there was no evidence of pregnancy or fresh uterine scars. Evernden (1966) reported that in C. gapperi mature follicles appeared in the ovary about 18 days after the vagina first became perforate. A female was considered in breeding condition if embryos or fresh uterine scars were present. A male was presumed in breeding condition if the testes were longer than 8 mm. and descended into the scrotum (Kalela, 1957).

Aging of autumn specimens was not attempted beyond the separation of those females which had borne a litter during the previous summer from those which had not. The two groups could be easily identified by the presence or absence of uterine scars in both species of Clethrionomys and P. maniculatus.

Female P. maniculatus of the spring populations which had overwintered were separated from those of the first spring litters, the young of the year. It was not necessary to separate overwintered females of Clethrionomys spp. from young of the year, as trapping terminated prior to the emergence of new litters at both Edmonton and Heart Lake. Separation of young of the year from overwintered adult P. maniculatus was accomplished by examination of reproductive condition, pelage, and body dimension. Young of the year were a uniform gray on the back and sides except for a distinct dorsal stripe. Adults were darker dorsally with a light brown color laterally, as described by Collins (1923). At both Edmonton and Heart Lake, young of the year had not become pregnant by the time trapping was terminated. Thus, overwintered females could also be identified by the presence of embryos or uterine scars.

To study overwintering changes in weight and growth rates, body dimensions and weights of fall, winter, and spring specimens of each species were compared. Duncan's new multiple range test (Steele and Torrie, 1960) was used to test for significance if 3 or more means were being compared. The test required equal numbers of variates in each subclass. Since my sample sizes were not equal initially, animals for use in the test were chosen by mixing the data cards and choosing the required number from the top of the deck.

Weather

Aerial and ground surface temperature were recorded continuously with a Yellow Springs Instrument Sequencing Telethermometer (Model 80) and recorder (Model 47) placed near the activity experiments. At

Edmonton, ground surface temperatures were recorded about 2 cm under the surface of the leaf litter; at Heart Lake about 2 cm under the surface of the lichen cover. Air temperatures were recorded 1.5 meters above the surface of the forest floor by means of a thermistor sheltered from direct radiation by spruce boughs.

Solar illumination was recorded continuously at both latitudes using Rustrak recorders and Silicon solar cells combined into field instruments. Two types of instruments were built by the Technical Services of the University of Alberta in cooperation with the author. The first type was abandoned after the first year of study at Edmonton due to problems arising during cold weather. An improved instrument was designed and built for the northern experiments. For calibration of foot candles, a Weston Mark IV Light Meter was used. The sun meters were placed 25 inches above the forest floor, adjacent to the activity cages.

To analyze the light data, 4 successive stages of illumination were chosen arbitrarily. Due to the difference in instruments, the chart ranges used differ at the 2 latitudes. The average number of hours of light at the 4 ranges were computed by 2 weeks periods. The Edmonton data represent light incident from the southern horizon. The Heart Lake data, taken with an improved instrument, represent light incident from 360° .

The use of foot candles is of dubious value (Evernden, 1966), and the problem of accurate measurement of light in wooded habitat is complicated by sun flecks, the thickness of the canopy, and the angle of the sun (Anderson, 1966; Evans, 1966; Weins, 1968). But in the

absence of a measuring device standardized to the spectral response curve of rodent eyes, foot candles give a standard for comparison (Collingbourne, 1966).

Certain characteristics of the snow cover which are thought to have a bearing on the microclimate in which the animals were living (Pruitt, 1957; Coulianos and Johnels, 1962; Formosov, 1964; Johnson, 1954) were measured with instruments designed by the National Research Council following the methods of Klein, Pearce and Gold (1950). These data are presented in Fuller, Stebbins, and Dyke (1969).

RESULTS

Weather

Winter at Edmonton was characterized by a frequent alternation of periods of relative cold and thawing (Figure 1). The coldest subnivean temperature ($-11^{\circ}\text{C}.$) was recorded in early January, 1965. Subnivean temperatures rose above freezing in mid-January, 1965, and remained between $-6^{\circ}\text{C}.$ and $+1^{\circ}\text{C}.$ until loss of snow cover in early April.

Aerial and subnivean temperatures at Heart Lake were much colder (Figure 2). Subnivean temperatures did not rise above $-5^{\circ}\text{C}.$ between November 18, 1965, and March 26, 1966. Between late December, 1965, and February 20, 1966, subnivean temperatures were between $-9^{\circ}\text{C}.$ and $-13^{\circ}\text{C}.$ April temperatures at Heart Lake were nearly as cold as January temperatures at Edmonton.

Snow depths were recorded in some of the trapping areas at Heart Lake and Edmonton (Figure 3). At Edmonton, continuous snow cover lasted 4 1/2 months, appearing about November 18, 1964, and disappearing in the first week of April, 1965. Snow cover lasted 6 months at Heart Lake, appearing in early November, 1965, and disappearing in the first week of May, 1966.

Seasonal variation in photoperiod and level of illumination differed greatly between Edmonton and Heart Lake (Figures 3, 4, and 5). Four ranges of illumination were chosen arbitrarily, and are indicated as 4 ranges of chart readings. One should note the relatively long duration of the highest level of illumination in winter at Edmonton (Figure 4).

A decrease in duration of that level of illumination began as a result of loss of snow cover in early April, and continued through May and June, probably as a result of foliation of the deciduous trees. A decrease in duration of the second highest level of illumination also occurred in May and June and the relative durations of the 2 lowest levels of illumination increased correspondingly. In contrast, one sees the brightest level of illumination lasts a relatively short time in winter at Heart Lake (Figure 5), but a relatively long time in spring.

Differences between the relative durations of the higher levels of illumination at the 2 latitudes result from differences in the nature of the plant cover and differences in photoperiod and light intensity. In winter in the boreal forest near Heart Lake, daylight is of short duration, and even on cloudless days, the light is quite dim because of the low angle of the sun's rays. Light penetrating to the surface of the snow is further reduced by presence of the coniferous canopy. In winter, in the deciduous forests near Edmonton, daylight lasts about 2 hours longer than at Heart Lake and is much brighter because of the greater angle of the sun's rays and the lack of deciduous foliage. In late spring, the situation is reversed. The duration of daylight is 4 hours longer at Heart Lake than Edmonton, and the deciduous canopy at Edmonton intercepts more light than that of the jack pine (Pinus banksiana) community in which the Heart Lake activity experiments were conducted.

Aerial light measurements are not representative of the subnivean

environment of the rodents in winter, late fall, and early spring. Thus it may be said they are of limited value for interpretation of activity data recorded under snow cover (Evernden, 1966). However, occasionally in winter, and frequently in spring and fall, the species of rodents studied come onto the snow surface. Such a brief exposure to light is probably all that is necessary as a zeitgeber (time cue) for phase control of circadian rhythms (Menaker and Eskin, 1967).

Though these data represent only bimonthly averages of arbitrarily chosen levels of illumination, they give some idea of seasonal and latitudinal variations in light conditions to which forest rodents are exposed.

Clethrionomys gapperi, Heart Lake

C. gapperi was nocturnal at Heart Lake during November and December, 1965, and May and June, 1966 (Figures 6 - 10). A bimodal peak of activity occurred shortly after dark in winter and persisted through the first 6 hours of darkness (Figure 6). A similar pattern occurred in May (Figure 7), but the general level of activity was higher. The distribution of activity during the peak was still bimodal in June (Figure 8), but note that it persisted through the first 6 - 8 hours of daylight the following morning.

Figures 9 and 10, transcriptions of the raw data from the individual C. gapperi tested at Heart Lake for the dates of May 28

through June 1, 1966, and November 16 - 19, 1965, illustrate the bimodal distribution of activity of individual animals during the peaks. In winter two distinct periods of activity occurred, each lasting about one hour and being separated by about two hours. In spring the periods of high activity started at hour 2000 and continued until dawn, about hour 0230. Then, after a 2 hour interval of very little or no activity, high activity resumed for 3 hours. Comparison of Figures 6, 7 and 8 indicated that the level of activity was generally much higher in spring than winter.

Clethrionomys gapperi, Edmonton

C. gapperi from Edmonton had definite early morning peaks of activity in winter, spring, and early summer (Figures 11 - 19). In November, December, and January a peak of activity occurred in the early daylight hours (Figures 11, 12, and 13). The morning peak of activity was present but not consistent during the remaining winter months (Figures 14 and 15). A relatively definite peak of activity returned in the early daylight hours of April, May, and June (Figures 16 and 17).

Seasonal changes in distribution of activity during the morning peak of activity occurred. The distribution was unimodal in November and December, 1964, and January, and the first half of March, 1965. Considerable variation occurred in the other winter

months. Figure 17 shows the development of a bimodal distribution of morning activity in the months of May and June, 1965. The bimodality began to develop in the last half of May, and continued through the month of June. The duration of the morning peak increased by about 4 hours.

Figures 18 and 19, transcriptions of the raw data from the individual C. gapperi tested at Edmonton for the dates of December 21 and 22, 1964, and June 23 - 27, 1965, illustrate the distribution of activity before, during and after the peaks. In December, a period of activity lasting less than an hour occurred near dawn. Very little activity occurred for about 2 hours before and after the peak. The activity was not this highly synchronized every day. In June, the periods of high activity started at dawn and continued periodically for about the next 7 hours.

In late fall and winter, the level of activity was generally lower than in spring. Activity for all daylight hours increased markedly in early May, and continued to increase through the end of June (Figure 17).

C. gapperi, Experimental Transplant to Edmonton

Activity experiments upon C. gapperi from Heart Lake were conducted at Edmonton in November and December, 1964. The results (Figures 20, 21, and 22) indicate C. gapperi of the Heart Lake region, when displaced from their own latitude to the more southerly latitude

of Edmonton, had daily patterns of activity in November and December very similar to those of the red-backed voles from the Edmonton region.

C. rutilus, Heart Lake

The distribution of activity of C. rutilus in winter was probably polyphasic (Figure 23), although there may have been a low peak at 1800 hours. In spring, a definite circadian rhythm, with a nocturnal pattern of activity, occurred (Figures 24 and 25). The daily peak of activity began about an hour before the onset of darkness and persisted into the first hour of daylight the following morning. A nocturnal peak of activity was present but not clearly defined in the first 2 weeks of May, but the level of nocturnal activity increased markedly during May, and continued to increase until mid-June. The level of activity during daylight was slightly higher in May than in either June or November and December.

Peromyscus maniculatus, Heart Lake

Results of P. maniculatus activity experiments conducted from November, 1965, to June, 1966, at Heart Lake are given in Figures 26 - 30. Activity records between January 11 and March 1 are missing because in mid-January the deer mice moved their nesting material out into the snow. Each time the nesting material was replaced in the nest box the mice removed it. The insulation was removed from the outside of the nest box in late February. After the removal of the

insulation, except for one short break, the deer mice nested in the nest box until the middle of June. It is not known if the deer mice started to nest in the nest box again because the insulation was removed.

Between December 15, 1965, and April 1, 1966, a higher level of activity occurred during dark than light hours (Figures 26, 27, and 28). Termination of higher activity was not well synchronized with dawn. The level of nocturnal activity remained quite low throughout this period.

In late March a well defined, bimodal peak of activity appeared (Figure 28). As spring progressed (Figures 28 - 30) the peak began earlier in relation to the beginning of darkness in evening and stopped later in relation to the end of darkness in morning. It first extended into the daylight hours in mid-April (Figure 29). This trend continued through the middle of June, when darkness lasted only 3 hours. Of particular note here is the extension of the peak of activity 7 hours into the morning daylight period in late May and early June.

The level of activity increased markedly from winter to summer, the time of change being concurrent with the first spring warming trend (Figure 28).

Growth and reproduction

Studies of changes in length and weight of wild individuals were made concurrently with the studies of activity to look for

relationships between changes in rate of growth and changes in patterns of activity. A rapid increase in rate of growth might be related to an increase in activity associated with foraging. Conversely, a slow rate of growth might be associated with low activity. Since, in Clethrionomys rufocanus, an increase in growth rate is associated with the onset of reproduction in spring (Kalela, 1957), studies of changes in reproductive condition were also made.

Growth of C. gapperi was studied at Edmonton in fall, winter and spring of 1964 - 1965. Results are shown in Table 1. No significant increase in total length occurred between November 20, 1964, and the end of April, 1965. May and June animals were significantly longer than those taken in any of the previous months. Changes in weight followed a similar pattern, but the animals slowly increased in weight in November, December, January, and February. A larger and more rapid increase occurred in May, concurrent with the rapid increase in length.

Results of studies of winter growth patterns of C. gapperi at Heart Lake are given in Table 2. No significant increase in total length or weight occurred between October and December, 1965, but in May, 1966, animals were significantly larger than those of the previous fall in both measurements.

Growth of C. rutilus was studied at Heart Lake in fall, winter, and spring of 1965 - 1966. The results are given in Table 3. The October, 1965, animals were significantly heavier than those taken in November, 1965. No significant increase in total length or weight occurred between October, 1965, and the end of March, 1966. May, 1966, specimens were significantly larger in both measurements.

Table 1. Significance test comparing weight and total length of *C. gapperi* taken at Edmonton in winter and spring, 1964 - 1965. In each test group, n = 24 (12 males and 12 females).

Code	Date	Mean weight	Mean total length
1	Nov. - Dec., 1964	12.53 ⁺ .24 g*	113.21 ⁺ 2.50 mm
2	Jan. - Feb., 1965	14.09 ⁺ .22 g	115.08 ⁺ 1.04 mm
3	March, 1965	15.30 ⁺ .24 g	115.71 ⁺ 1.04 mm
4	April, 1965	15.91 ⁺ 1.18 g	115.07 ⁺ 1.18 mm
5	May, 1965	20.77 ⁺ .54 g	126.50 ⁺ 1.09 mm
6	June, 1965	23.83 ⁺ .71 g	129.58 ⁺ 1.30 mm

1 is significantly lighter than 2 at the 5% level.

2 is significantly lighter than 3 at the 5% level.

4 is significantly lighter than 5 at the 1% level.

5 is significantly lighter than 6 at the 5% level.

5 and 6 are significantly longer than 1,2, 3, and 4 at the 1% level.

* ⁺ standard error

Table 2. Significance test comparing weight and total length of C. gapperi taken at Heart Lake. In each test group, $n = 12$.

Code	Date	Mean weight	Mean total length
1	October, 1965	15.9 ± 1.65 g*	118.7 ± 1.25 mm
2	November and December, 1965	16.1 ± 0.54 g	119.5 ± 1.94 mm
3	May, 1966	22.9 ± 0.91 g	137.3 ± 1.33 mm

3 is significantly heavier than 1 and 2 at the 1% level.

3 is significantly longer than 1 and 2 at the 1% level.

* \pm standard error

Table 3. Significance test comparing weight and total length of C. rutilus taken at Heart Lake. In each test group, $n = 12$.

Code	Date	Mean weight	Mean total length
1	October, 1965	16.6 ± 0.40 g*	114.4 ± 1.67 mm
2	November, 1965	14.8 ± 0.45 g	113.2 ± 1.20 mm
3	February and March, 1966	15.5 ± 0.51 g	115.5 ± 1.38 mm
4	May, 1966	19.6 ± 0.93 g	125.3 ± 2.10 mm

1 is significantly heavier than 2 at the 1% level.

4 is significantly heavier than 1, 2, and 3 at the 1% level.

4 is significantly longer than 1, 2, and 3 at the 1% level.

* \pm standard error

Growth of P. maniculatus was studied at Heart Lake in 1964, 1965, and 1966. Female deer mice taken in May, 1966, were divided into 2 classes, parous or pregnant, and not parous or pregnant. Because these 2 classes were significantly different in weight and total length, and because male deer mice could not be so classed, only females were used for analysis of growth for the winter of 1965 - 1966. This was not necessary or possible in Clethrionomys spp. because, in that genus, at neither Edmonton nor Heart Lake was there evidence of subnivean reproduction or of 2 size classes among the females taken in spring.

Data in Tables 4 and 5 indicate that in April, 1965, male and female P. maniculatus were significantly heavier and female P. maniculatus were significantly longer than those of the previous fall. The females were, however, about 20 mm shorter and 4 g lighter than reproducing females taken in May the following year (Table 6), indicating considerable growth had yet to occur before they attained the size of adult summer animals.

All parous or pregnant females taken in May, 1966 were tested separately from those not parous or pregnant taken in May. For convenience the parous or pregnant females were called reproducing females, the others, non-reproducing females. Results of the 1965 - 1966 studies are given in Table 6. Two distinct size groups were present in the May, 1966, population. The parous and pregnant females were comparable in weight and total length to the adult summer deer mice taken by Soper (1964) 100 miles East of Heart Lake. The non-parous females were not significantly different in weight or total length than those taken during the previous October.

Table 4. Significance test comparing weight and total length of P. maniculatus females taken at Heart Lake in the winter of 1964 - 1965. In each case, $n = 12$. None of the females was parous or pregnant.

Code	Date	Mean weight	Mean total length
1	October, 1964	$13.3^{+} 0.4 \text{ g}^{*}$	$136.0^{+} 2.10 \text{ mm}$
2	April, 1965	$15.6^{+} 0.5 \text{ g}$	$145.6^{+} 2.77 \text{ mm}$

2 is significantly heavier than 1 at the 1% level.

2 is significantly longer than 1 at the 1% level.

* $^{+}$ standard error

Table 5. Significance test comparing weight and total length of P. maniculatus males taken at Heart Lake in the winter of 1964 - 1965. In each case, n = 12.

Code	Date	Mean weight	Mean total weight
1	October, 1964	$16.7^{\pm .66} \text{ g}^*$	$157.3^{\pm 2.7} \text{ mm}$
2	April, 1965	$19.4^{\pm .57} \text{ g}$	$150.3^{\pm 2.3} \text{ mm}$

1 is significantly lighter than 2 at the 1% level.

2 is not significantly different than 1 in total length.

* \pm standard error

Table 6. Significance test comparing weight and total length of P. maniculatus females taken at Heart Lake in the winter of 1965 - 1966. In each test group, n = 12.

Code	Date	Mean weight	Mean total length
1	October, 1965	14.1 ± 0.25 g*	149.1 ± 2.0 mm
2	May, 1966, non-reproducing females	15.2 ± 0.39 g	153.2 ± 1.45 mm
3	May, 1966 reproducing females	19.3 ± 0.74 g	165.9 ± 2.17 mm

3 is significantly heavier than 1 and 2 at the 1% level.

3 is significantly longer than 1 and 2 at the 1% level.

* \pm standard error

As will be discussed in the next section, the deer mice began to reproduce under the snow in late winter. The young from these early litters likely composed the immature segment of the May, 1966, population. The reproducing members likely represented mice which overwintered.

Table 7 gives detailed reproductive data of female red-backed voles caught during the Edmonton studies. The fall, 1964, population was composed primarily of the "immature phase" (Kalela, 1957). By the first week in June, 1965, all overwintered females captured were either pregnant or had recently given birth. Since snap-trapping indicated that the young had left the nests by June 7, an event which normally occurs about 17 days after birth (Peterson, 1966), the first litters were born sometime after May 22.

Reproductive data of female C. gapperi trapped at Heart Lake are also given in Table 7. Trapping was terminated prior to the occurrence of the first spring pregnancies during both years of the Heart Lake experiments. According to Fuller (in press), who trapped continuously in that area during the summers of 1965 and 1966, the first visible pregnancy was recorded on May 25 in 1965.

In the spring of 1966, my trapping terminated on May 22, the day on which Fuller (op. cit.) captured the first visibly pregnant C. gapperi. Conception probably occurred about May 16, and the first young of the year were taken by Fuller on June 20.

Fuller (op. cit.) estimated that first conceptions in C. rutilus occurred about May 6 in 1965 and about May 5 in 1966. Young of the year were first taken by Fuller on June 10, 1965, and June 19, 1966.

Table 7. Summary of reproductive data of C. gapperi females taken at Edmonton and Heart Lake.

Date and location	Pregnant	Placental scars and lactating	Old placental scars	No placental scars
Edmonton				
Nov. - Dec., 1964	0	0	6	24
Jan. - Feb., 1965	0	0	3	32
March, 1965	0	0	0	16
April, 1965	0	0	0	17
May, 1965	0	0	0	9
June 1 - 6, 1965	5	4	0	0
Heart Lake				
Sept., 1964	0	0	0	2
April, 1965	0	0	0	2
Oct., 1965	0	0	0	8
Nov. - Dec., 1965	0	0	1	5
April, 1966	0	0	0	1
May, 1966	0	0	0	3

The October, 1964, population of P. maniculatus at Heart Lake was composed primarily of the "immature phase". Of 29 females captured, 3 were parous. The following spring, no pregnancies were recorded as of the termination of trapping on April 18, 1965. Fuller (op. cit.) estimated that first conceptions occurred about May 1, 1965. In the fall of 1965, the population was also composed primarily of the "immature phase". No females were taken which had borne young. The reproductive data for the mice emerging from the snow cover during the first week in May, 1966, show that there were 2 classes of females. In early May, 23% (20 of 85) of the females taken were parous or pregnant, whereas the remainder showed no signs of having bred. The morphological differences between these classes are shown in Table 6, and have been discussed. Two of the females were lactating. They had enlarged mammary glands and the hair directly surrounding the nipples had been worn away. Allowing 22 - 27 days of gestation, breeding must have begun in early April. Several males in breeding condition were taken in the first week of April when they emerged from under the snow during a few warm days. The testes of these males were scrotal in position, and sperm were seen in a smear made from the epididymis of one specimen.

DISCUSSION

Patterns of the Circadian Rhythms

At Heart Lake seasonal changes occurred in the circadian rhythms of all 3 species of rodents. Winter patterns were similar in C. rutilus and P. maniculatus in that no well defined peaks of activity occurred during winter, though P. maniculatus were more active during

dark than light hours. The winter peak of activity for C. gapperi began shortly after dusk and lasted about 4 hours.

At Heart Lake in spring the daily peaks of activity of each of the 3 species began from 1 - 2 hours before the onset of darkness. But the C. gapperi peak persisted from 7 - 9 hours into the daylight of the next morning, the P. maniculatus peak lasted from 4 - 5 hours into the daylight of the next morning, and the C. rutilus peak lasted about 1 hour into the daylight of the next morning. Thus the daily peak of activity of C. rutilus, C. gapperi, and P. maniculatus consisted to varying degrees of crepuscular, nocturnal, and diurnal activity. Numerous authors have reported similar seasonal differences in the activity of a variety of small rodents, but the phenomenon has not been explained. Miller (1955), Chitty and Shorten (1946), and Williams (1959), suggested that expression of a nocturnal or diurnal preference in a variety of animals is secondary to the satisfaction of basic food and energy requirements. This may apply here. In winter no reproductive activity occurs. Growth is very slow or arrested. The level of activity is relatively low. These factors presumably reduce the food and energy requirements of the animals, and may contribute to the reduction in winter of the duration and amplitude of the daily peak of activity in C. gapperi, and the apparent elimination of a peak in P. maniculatus and C. rutilus.

As spring progresses, reproduction begins, growth becomes more rapid, and the general level of activity increases. Food and energy requirements must rise accordingly. Perhaps increased foraging to meet the higher food and energy requirements occurs, but is primarily

limited to certain hours of the day, thus contributing to the development of the well defined circadian rhythms of activity in early spring.

Reasons for the specific differences in extension of the peaks of activity into the daylight hours of morning in spring are unknown. Two factors of possible importance are differences in the preference for nocturnal, as opposed to diurnal activity, and differences in ability to meet energy requirements. It appears that C. rutilus have the ability to satisfy their requirements with much less exposure to bright daylight than P. maniculatus, normally considered nocturnal, and C. gapperi.

C. gapperi at Edmonton were mainly diurnal in spring, summer, and most of winter. Differences in the circadian rhythms of Edmonton and Heart Lake populations of C. gapperi are unexplained. That the normally nocturnal animals from Heart Lake had a diurnal activity pattern when tested at Edmonton indicates the pattern is flexible, and perhaps learned or perhaps a response to some environmental component associated with latitude, particularly photoperiod or interactions between C. gapperi and C. rutilus in the Heart Lake region.

Viewed in one way, the circadian rhythms of C. gapperi were basically similar at Edmonton and Heart Lake. In late spring at Edmonton, C. gapperi were quite active during the hours of dim illumination in evening and early morning, and on into the brighter daylight of mid-morning. In late spring, C. gapperi at Heart Lake were also active during these periods of dim illumination, and on into early hours of daylight. Thus at Heart Lake, the peak of activity

associated with the dim illumination of late evening is continuous, or nearly so with that associated with the dim illumination of early morning. Viewed in this way, C. gapperi would be considered crepuscular with an extension of activity into the daylight hours of morning, in spring, at both latitudes.

It might be advantageous for C. gapperi, along the zone of contact with C. rutilus, to have daily peaks of activity concurrently with those of C. rutilus. If the majority of foraging and nesting activity occurs during the time of peak activity, survival or distribution of either species might be associated with defence of favorable nesting sites and competition for food sources. Further studies of the daily distribution of types of behaviour, interactions between the two species, and geographical distribution of nocturnal circadian rhythms in C. gapperi seem necessary to the complete explanation of this phenomenon.

Levels of Activity

In spring, levels of activity increased during light and dark hours for all 3 species studied. This might have resulted from the previously mentioned seasonal changes in energy requirements associated with reproduction and growth, or from other environmental factors.

Several authors have shown a relationship between nutritional levels and activity levels of rodents. A direct relationship between food supply and level of activity of Palearctic rodents was reported by Koshkina (157). She observed an increase in activity of C. rutilus and C. glareolus in fall, when their food supply became scarce. She says, "In the case of the European vole (C. glareolus) activity increases

in late autumn, which is connected with the impoverishment of food supplies at this time and possibly also with the storing of food. The European vole is obliged to run about more in search of lichen and rare seeds, it climbs up trees, and in winter comes not infrequently onto the surface of the snow. Therefore, it is subjected more often than the red-gray vole (C. rufocanus) to attacks by predators and to the influence of unfavorable meteorological conditions".

Wald and Jackson (1944) reviewed several papers which showed an increase in activity in many taxa of animals during hunger, and pointed out that presence of hunger contractions is not necessary to this phenomenon. They reported that a deprivation of food, water, both food and water, or thiamine would greatly increase running activity in caged white rats. They concluded, "The primary response to food deprivation is activity as such...", and not food seeking, but that activity will increase the probability of food encounters in the free environment.

Grodzinsky (1960) has shown that caloric content of food has a marked and rapid influence on the amount and pattern of activity of the normally nocturnal Apodemus sylvaticus, Microtus agrestis, and Clethrionomys glareolus. Each species showed more diurnal activity and more frequent bursts of feeding activity as caloric content decreased. Calhoun (1945) reported that complete food deprivation caused the peak of activity to occur earlier, and total activity to increase in the cotton rat, Sigmodon hispidus.

If experimental manipulation of nutrition can affect levels of activity, it is probably true that changes in the energy budgets

of individuals of natural populations can affect their nutritional needs, and also their levels of activity. Seasonal changes in growth and reproduction might have this effect. Kalela (1957) reported a close relationship between seasonal changes in growth and reproduction of C. rufocanus in Finnish Lapland. He found that nearly all voles born in the first litters of summer became sexually mature that summer. They reached a weight of between 20 and 24 grams by the age of one month, at which time sexual maturation began. Their growth rate continued "unlimited" during summer. Mature summer adults reached a weight of between 30 and 55 grams. The sexual maturation of the second and third litters of the summer varied with duration of the breeding season and with sex, but there was always a tendency for the majority of them to remain sexually immature until the spring of the next year. The growth of those remaining immature stopped at a weight between 20 and 24 grams, the weight at which they entered winter. Voles of this weight predominated in the September population. Kalela called this the "immature phase" or the "winter phase" of the voles. A rapid growth rate commenced again with the onset of sexual maturation in spring. He also observed that "...the bulk of individuals which had attained sexual maturity in the year of their birth die before the next breeding season". The latter observation is supported by several other authors (Gunderson, 1962; Schwartz et al., 1964; Sealander, 1966; Sealander and Bickerstaff, 1967).

The C. gapperi studied at Edmonton seem to fit the overwintering pattern of growth and reproduction described by Kalela for C. rufocanus.

Judging from the weight distribution and the reproductive data for the females (Table 7), the majority of animals in fall were of the immature phase described by Kalela. They remained sexually immature and ceased rapid growth in summer at a weight between 12 and 14 grams. This is the weight at which early summer litters reached sexual maturity. Growth again became rapid when sexual maturation began the following spring.

Changes in weight and length of C. gapperi taken at Heart Lake indicate a pattern similar to that of C. gapperi at Edmonton. The fall, 1965, population was also composed primarily of animals of the immature phase.

C. rutilus had a winter pattern of growth similar to that of C. gapperi. Death of older members of the population may have caused the mean weight of the specimens of October, 1965, to have been significantly heavier than those of November, 1965. This was reported for C. rutilus by Sealander and Bickerstaff (1967).

Changes in weight and length of P. maniculatus at Heart Lake were basically similar to those of both species of red-backed vole.

Schwartz et al. (1964) showed that an arrested growth in winter is accompanied by a decrease in adrenal and kidney weights in a variety of rodents. These organs increased in weight again with increased growth rates and sexual maturation in spring. He concluded that a decrease in basal metabolism occurred in winter. Pearson (1962) showed a decrease in basal metabolic rate for C. glareolus in winter, Scholander et al. (1950) and Hart and Heroux (1955) have shown the same for the lemming (Dicrostonyx).

Considering the above results, it is not surprising that the animals in this study increased their levels of activity in spring when all 3 species studied had the metabolic burdens of an approximate 20% increase in size, an increase in activity associated with reproducing, and, for the females, pregnancy and nursing. The increased energy demands associated with reproductive behaviour, pregnancy and lactation could cause an increase in amount of activity required for foraging, and the reproductive behaviour itself could cause an increase in level of activity.

There is general agreement that temperature can affect circadian rhythms, but many authors report conflicting results. Pitymys subterraneus, exposed to both 18 and 6 hour days, had a higher level of activity in a cold (5°C.) than a warm (20°C.) environment (Gebczynski, 1964). He concluded that the control of the phase of the circadian rhythm is temperature independent, but the amplitude of the activity peak is temperature dependent. The periodicity of the circadian rhythm of Microtus pennsylvanicus became variable and the amplitude of the activity peak decreased below 0°C. (Hatfield, 1940). The frequency of feeding activity decreased. Bünning (1964) reviewed the evidence for the relationship between amplitude of peaks of activity and temperature, and concluded that amplitude is greatly dependent upon temperature and may even disappear with decreasing temperature, but will reappear, in phase, upon warming.

A decrease in the amplitude of the daily peaks of activity occurred in winter in all 3 species studied here, and no daily peak was apparent at all for C. rutilus in winter. However, this decrease may have been partially or wholly caused by other factors, particularly

growth, reproduction, and associated alterations in behaviour and energy budget rather than temperature. It is noteworthy though that rapid increases in amplitude in spring all coincided with rapid increases in soil surface temperature.

Another factor directly related to energy budget and activity is torpor. P. maniculatus underwent periods of daily torpor in winter at Heart Lake. This presumably reduced their energy budget (Lyman, 1964; Jameson, 1965). They had the lowest level of winter activity of the 3 species tested. During early January and early March there was almost no activity during the day and little at night. The deer mice were removed from their nest box while torpid and found to fit the description of torpid Peromyscus spp. as described in nature by Howard (1951). They were found asleep or lethargic, either in the nesting material or in the snow outside the nest. They had a slow breathing rate, moved their limbs slowly when walking, let their tails drag, and made no attempt to run or escape. When the temperature moderated somewhat in late March and early April, P. maniculatus were no longer observed in torpor, and their general level of activity increased considerably.

Responses to sexual stimulation can also cause changes in amounts of activity. An increase in the activity level of males in breeding season is a generally known phenomenon. Wald and Jackson (1944) demonstrated that female rats have a high level of activity during estrus, which ceases upon copulation or stimulation of the cervix. Increased activity during estrus was also reported for white rats, hamsters, horses, dogs, and cattle (Folk, 1966). Thus it is probable that the onset of reproduction in spring was at least partially

responsible for the increased activity recorded in these experiments.

Although I have been unable to find references in the literature, the growth of foliage in spring might alter the activity of rodents, particularly in deciduous forests. After loss of snow cover and before foliation, small forest rodents are exposed to higher levels of illumination during daylight hours than at any other time of year. Exposure to avian predators is also greater at this time of year. Non-peak activity of C. gapperi increased at Edmonton between late May and early June, 1965 (Figure 17, 1100 to sunset). In this period a decrease in duration of illumination brighter than 300 foot candles occurred at a height of 56 cm above the forest floor (Figure 4). The decrease at the level of the forest floor was probably greater, because considerable vegetation existed below 56 cm.

No such change in illumination occurred at Heart Lake (Figure 5). The main canopy, of Pinus banksiana, was relatively thin and showed little seasonal change. Vegetation closer to the forest floor was sparse. The non-peak activity of C. gapperi at Heart Lake did not change radically after mid-May, although foliation began in late May (Figures 7 and 8, 0900 to sunset).

Short term cycles and Peaks of Activity

The short term cycles during non-peak hours of the day consisted of 10 - 20 minutes bursts of activity at 3 - 5 hour intervals. Shape of the curves depicting daily variations in levels of activity depended upon the distribution and duration of these periodic bursts of activity.

During non-peak hours of activity, the combined effect of the short bursts of activity of the several animals being tested produces a polyphasic pattern.

During peak hours of activity, 2 changes in the short term cycle occur. The duration of the short bursts of activity is extended and the extended bursts of activity tend to occur synchronously among different individuals. The findings of several authors support these data (Grodzynski, 1963; Pearson, 1962; Gebczynski, 1964). Seasonal changes in the daily peaks of activity can be ascribed to corresponding changes in the number of short term cycles involved in the peak activity and the duration of these bursts of activity.

This can best be seen in the data for C. gapperi because of their definite peaks of activity in winter. Figure 18 gives the raw activity data of C. gapperi at Edmonton on December 21 and 22, 1964. The data are transcribed onto graph paper from the original chart paper for the hours surrounding the morning peak of activity. This indicates that the sharp peak in the pattern of activity for the last half of December, 1964, (Figure 12) resulted from a slight increase in duration of one short term burst of activity at dawn, and the synchronized occurrence of that activity among all animals being tested. Such a high degree of synchronization did not occur every day, but often enough to produce a definite periodicity, or a circadian rhythm. This peak of activity was monophasic because only one short term cycle was involved. The very sharp nature of the peak resulted from the high degree of synchronization of the burst of activity among the animals tested.

Figure 19 gives the raw activity data of C. gapperi at Edmonton on June 23 - 27, 1965. The morning activity peak (cf. Figure 17) is a result of a relatively high level of activity for about 7 hours, or the duration of 2 - 4 short term cycles, the number varying between test animals. It is evident that there is a high degree of intraspecific variation in the short term cycle. This has been reported by many investigators.

In November at Heart Lake, C. gapperi had a bimodal peak of activity in which 2 or 3 short term cycles were involved. A comparison of Figure 6 and 9 indicates the relationship between the short term cycles and the bimodal peak of activity. One can see in the transcribed data that the occurrence of the short term cycles occurring in late evening corresponds to the 2 portions of the bimodal peak of activity indicated for C. gapperi in Figure 6. In early June at Heart Lake, C. gapperi had a bimodal peak of activity. The 2 peaks were separated by a period of low activity of about 3 hours (Figure 8). The raw data (Figure 10) indicate that at least for some of the test animals, the 2 peaks resulted from a succession of several short term cycles. The first group of cycles began before dark and persisted for about 7 hours. This was followed by a period of about 3 hours with little or no activity. This was followed by a third period of between 1 and 4 hours in which 1 or 2 short term cycles occurred.

Ecological Implications

In spring only about 65% of the duration of the daily peak of activity of C. gapperi occurs concurrently with the daily peak of C. rutilus and in winter C. gapperi has an obvious peak while C. rutilus

does not, therefore it does not seem that the circadian rhythms would greatly reinforce competition between the species. However, to ascertain the adaptive value of the seasonal, specific, and latitudinal differences in circadian rhythms reported here, or the degree to which circadian rhythms directly affect competitive exclusion between species, further studies of daily and seasonal distribution of such activity as food gathering and storing, nest cleaning and moving, and reproduction are required.

Presumably the various circadian rhythms encountered represent adaptation or acclimatization to a combination of environmental factors which vary with season and latitude: temperature, snow cover, photoperiod, illumination, energy requirements, predation and competition. In this study, the levels of activity, particularly during daily peaks of activity were generally reduced in winter. This was the time of lowest temperatures, shortest photoperiod, general protection by snow cover, and dimmest illumination. Perhaps these environmental factors decrease the need for high levels of activity and expression of circadian rhythms in winter. Some of them affect other facets of the life history of the species studied, and thus might indirectly control activity. In particular it has been suggested here that reproduction, winter and spring growth patterns, and torpor influence the circadian rhythms of the species studied by seasonally altering their energy demands.

Figure 1. Daily range of air and subnivean or leaf litter temperatures (degrees centigrade) for the winter and spring of 1964 - 1965 at Edmonton. A continuous record of the subnivean temperature was not started at Edmonton until January 4, 1965.

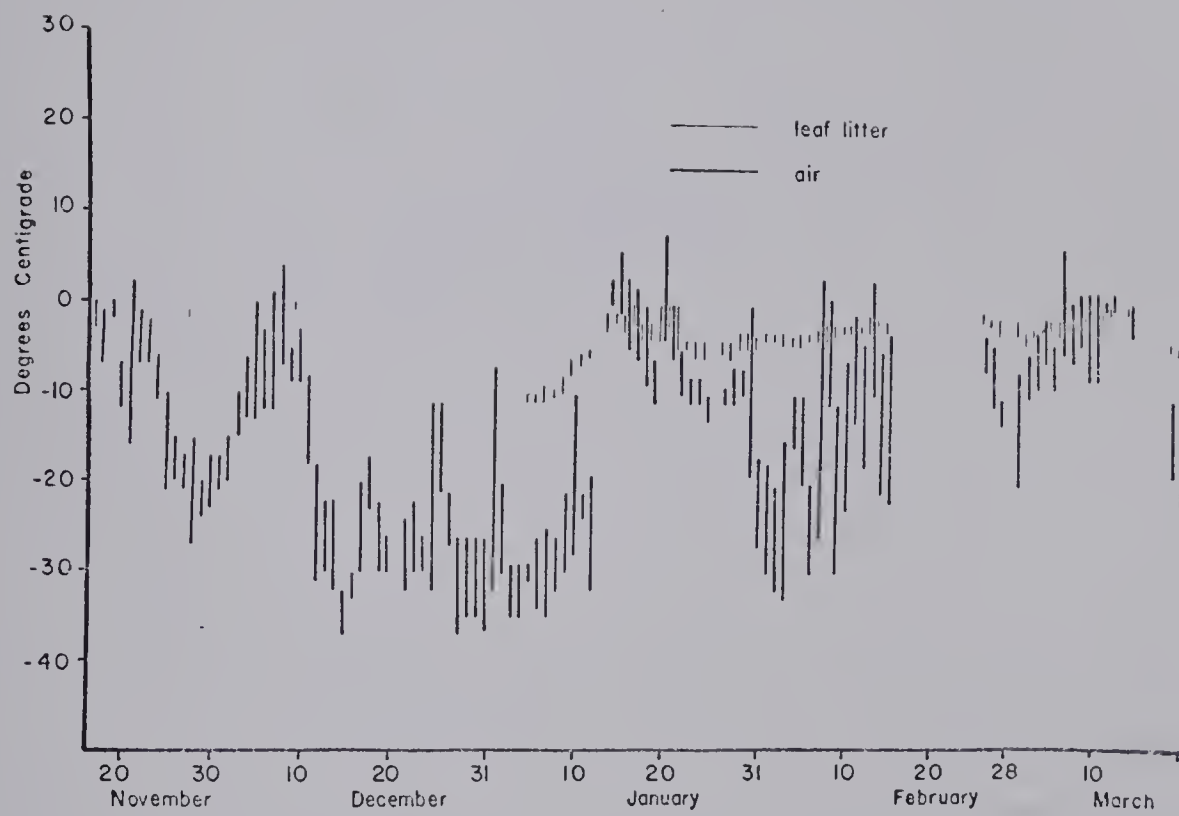


Figure 1. (continued).

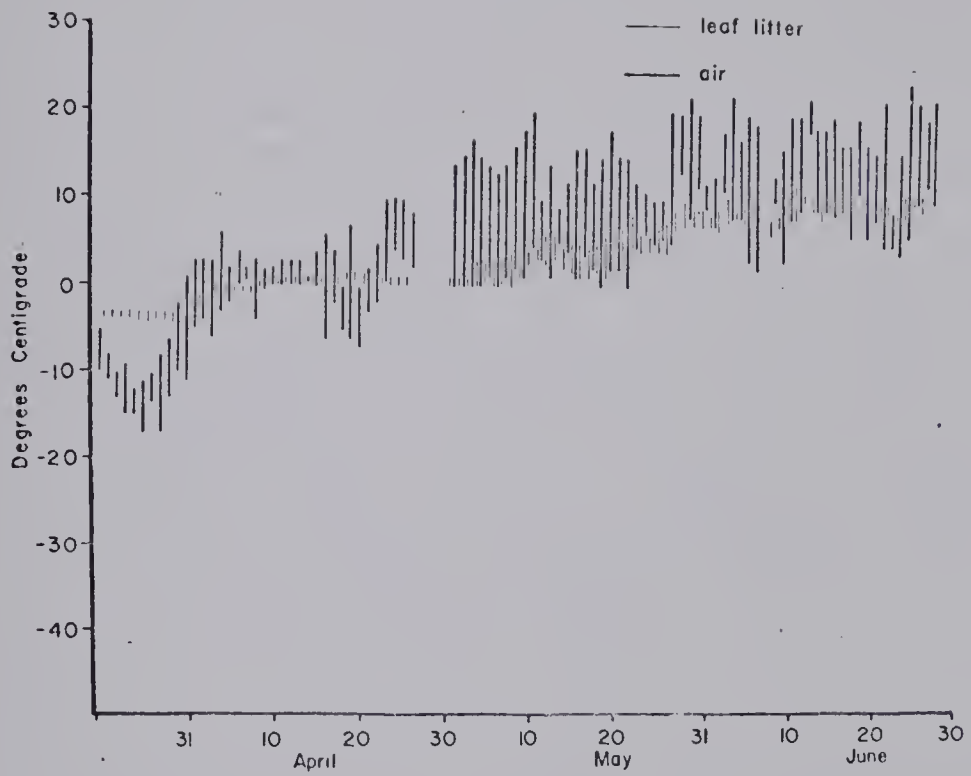


Figure 2. Daily range of air and subnivean temperatures at Heart Lake during the winter of 1965 - 1966 (degrees centigrade).

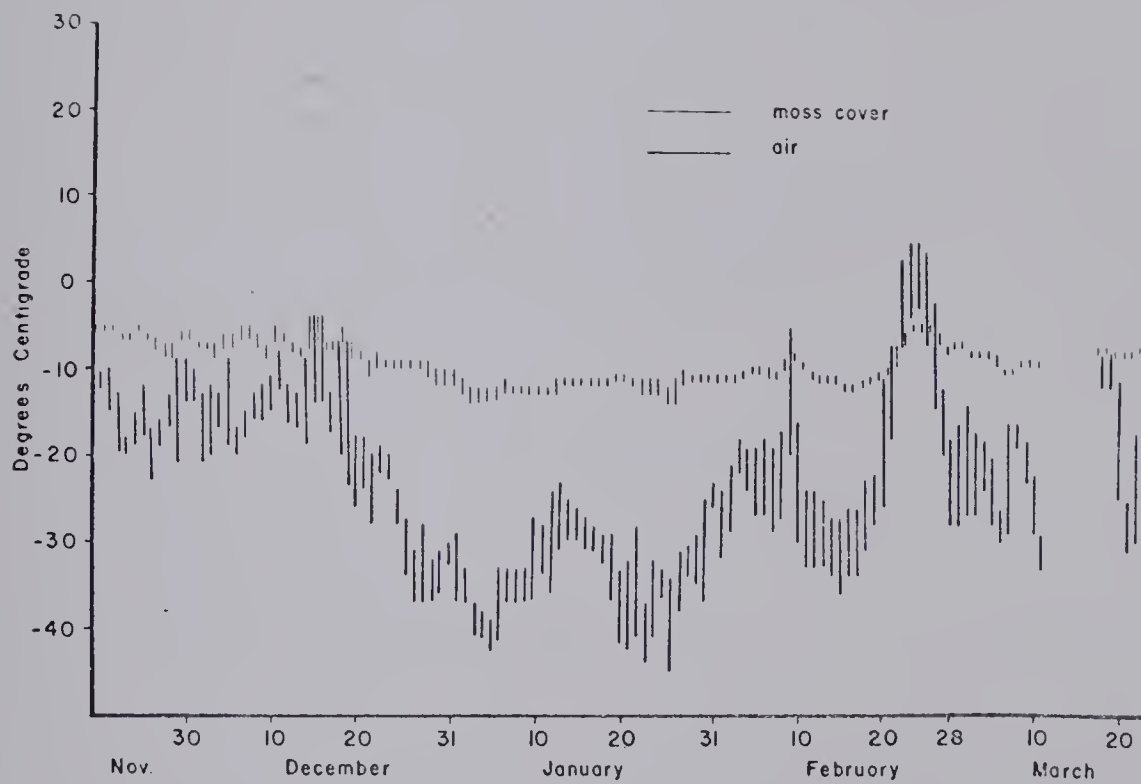


Figure 2. (continued).

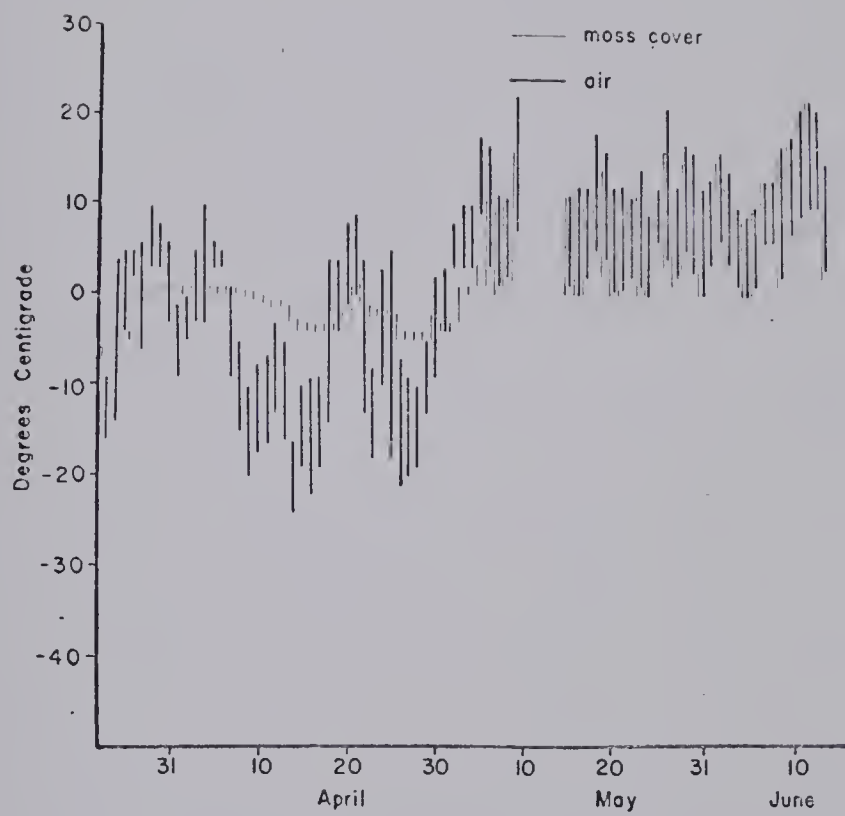


Figure 3. Hours of daylight (2-week averages) and depth and duration of snow cover during the winters of 1964 - 1965 at Edmonton and 1965 - 1966 at Heart Lake.

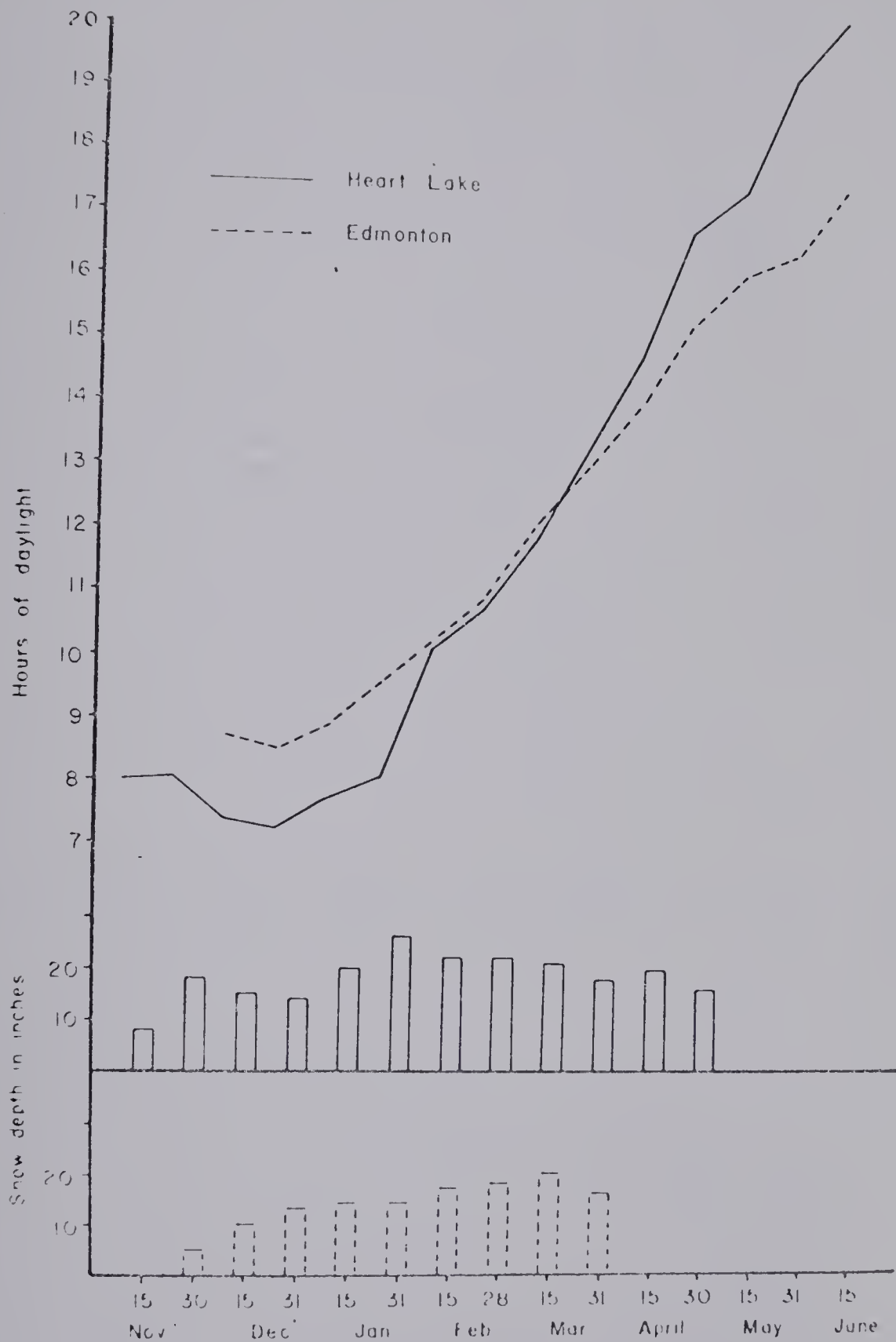


Figure 4. Duration of 4 ranges of chart readings indicating 4 levels of illumination during the winter and spring of 1964 - 1965 at Edmonton. Values are given as 2-week averages. Ranges in foot candles are given in parentheses.

Figure 5. Duration of 4 ranges of chart readings indicating 4 levels of illumination during the winter and spring of 1965 - 1966 at Heart Lake. Values are given as 2-week averages. Ranges in foot candles are given in parentheses.

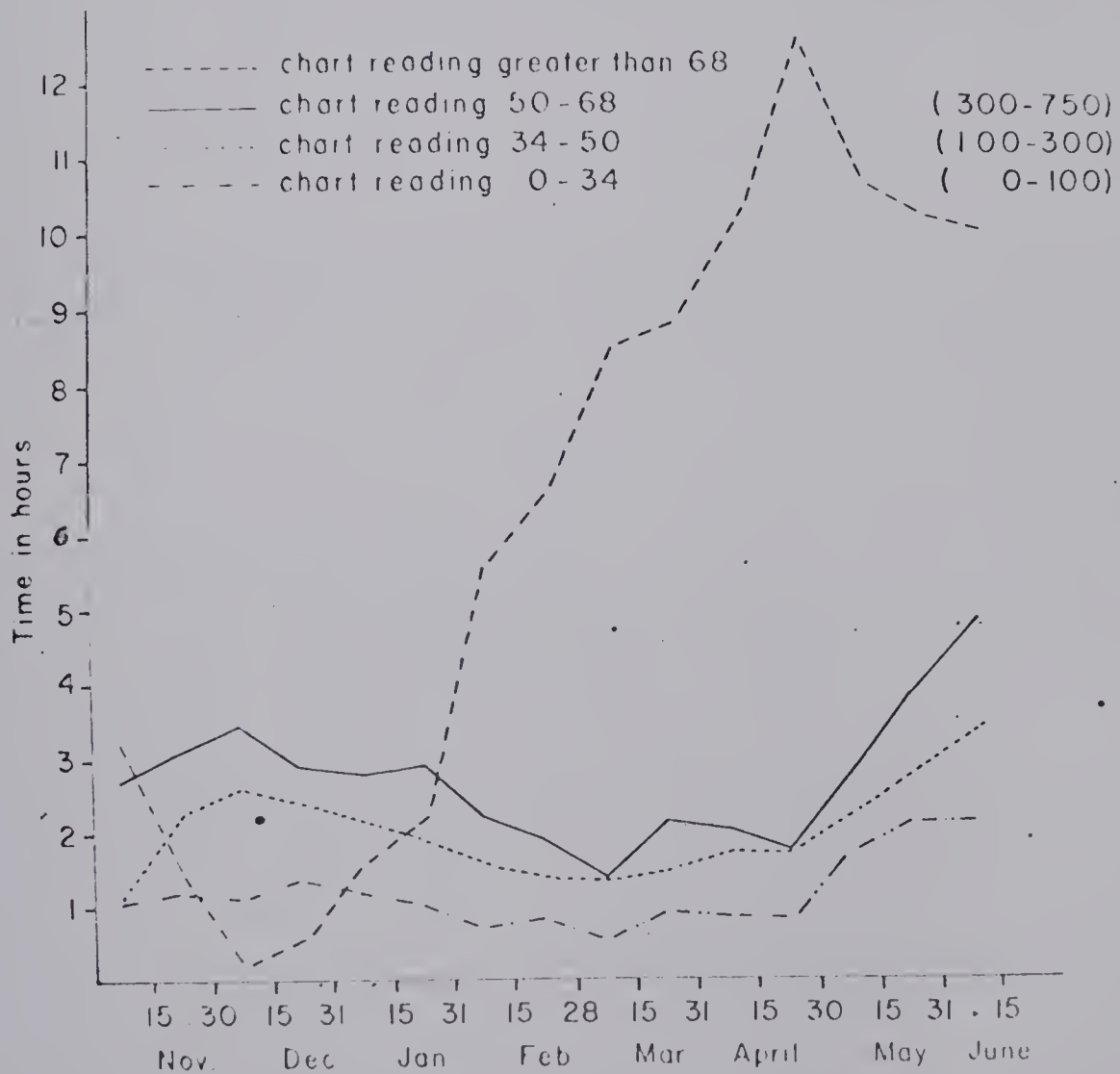
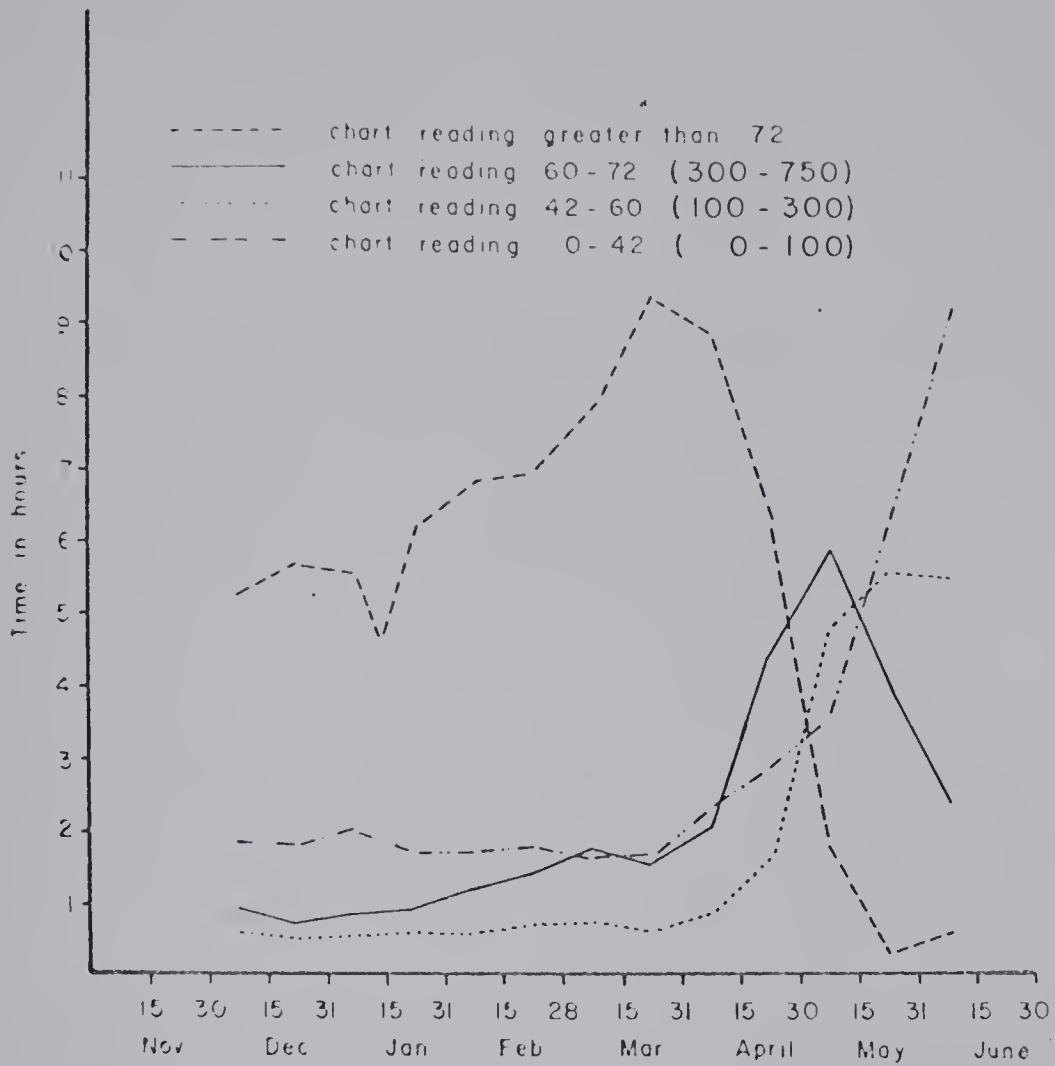


Figure 6. Daily activity patterns of C. gapperi from Heart Lake as tested at Heart Lake during November 16 - 30 and December 1 - 15, 1965. Two males and two females housed individually were tested. The term "average count" refers to the average number of times the gate at the entrance of the nest boxes was crossed by the test animals. Time is given with hour 0100 through hour 2400 abbreviated to hour 1 through hour 24. Periods of darkness are indicated by vertical stipled lines across the top of the graph. The short line with loops indicates the range of variation in photoperiod during the test period. The pattern of activity is nocturnal with a bimodal peak of between hour 16 and hour 22.

Figure 7. Daily activity patterns of C. gapperi from Heart Lake as tested at Heart Lake during May 1 - 15 and May 16 - 31, 1966. Refer to the legend for Figure 6 for details. The pattern of activity is nocturnal with a bimodal peak beginning just after dark.

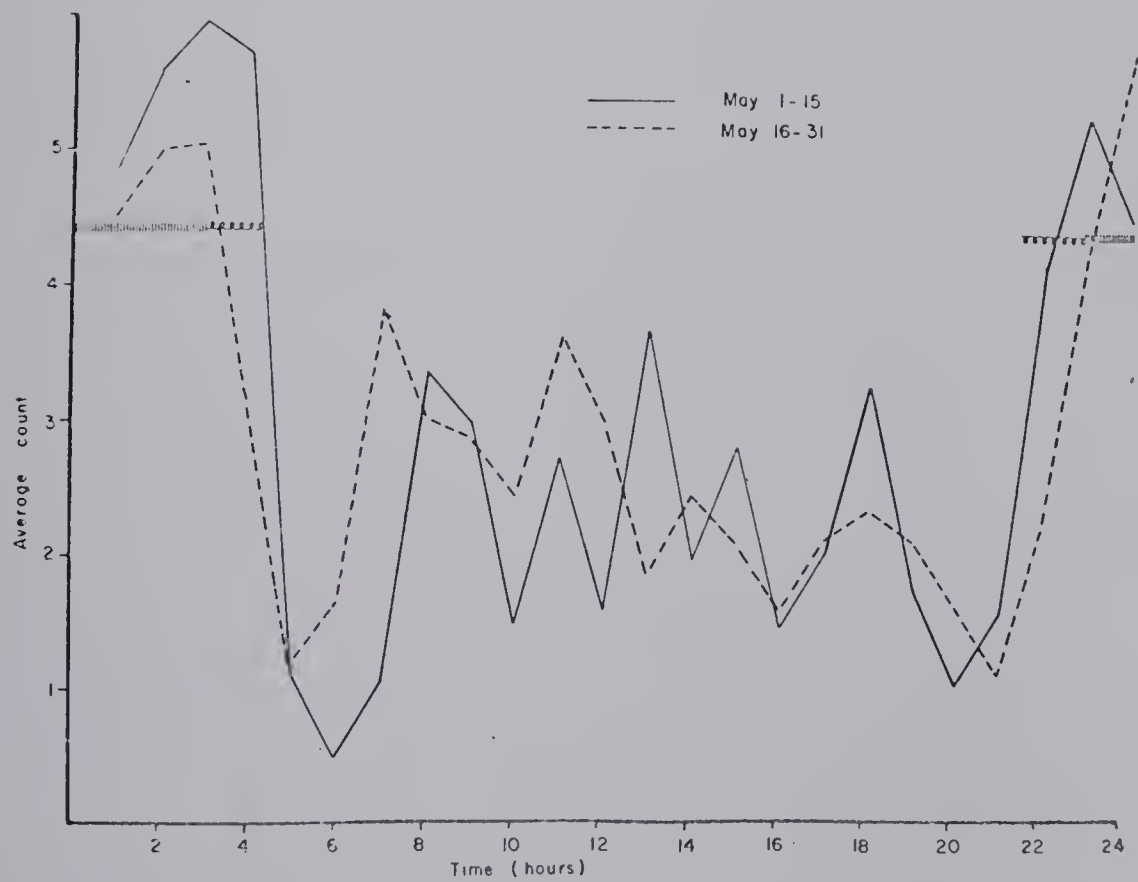
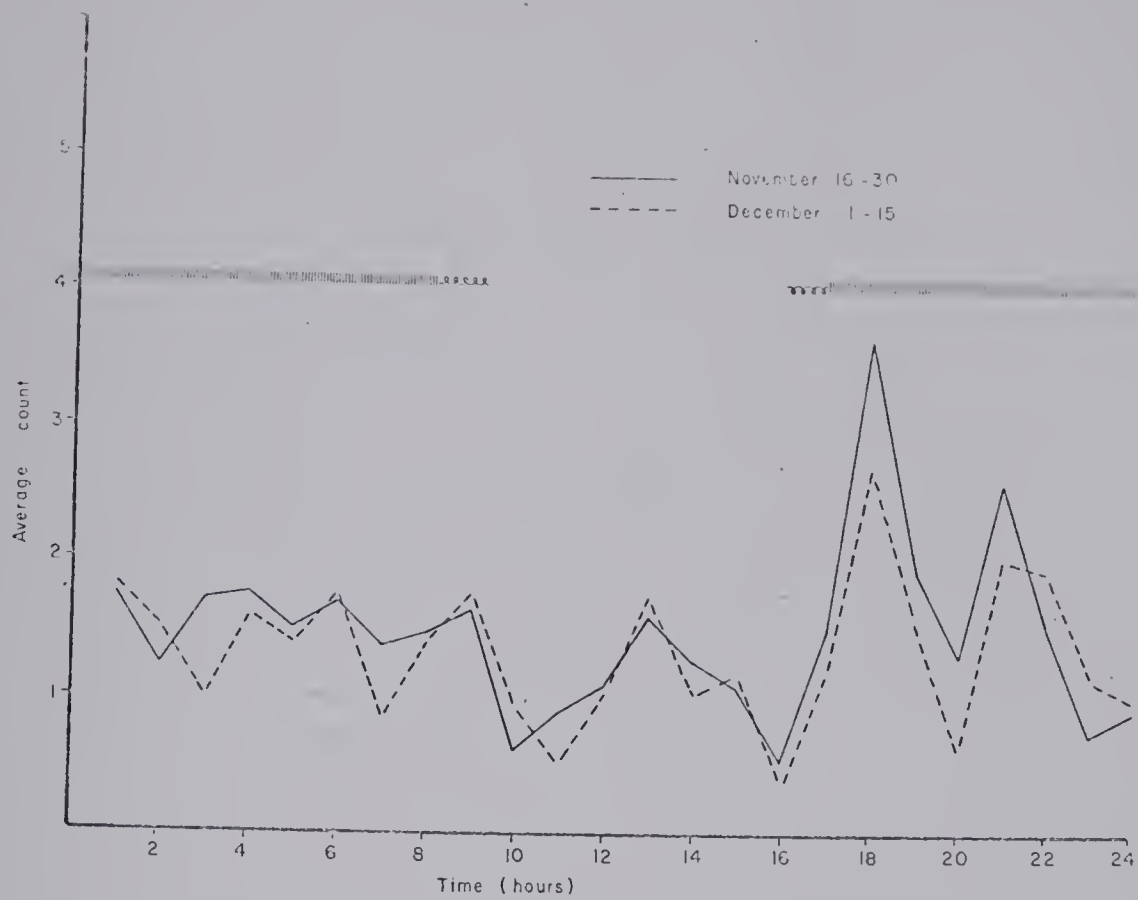


Figure 8. Daily activity patterns of C. gapperi from Heart Lake as tested at Heart Lake during June 1 - 15, 1966. Refer to the legend for Figure 6 for details. Two males and two females, housed individually, were tested. A bimodal peak of activity began in the dusk of late evening and persisted through the first 7 hours of daylight the next morning.

Figure 9. A transcription of raw data from activity charts of C. gapperi from Heart Lake as tested at Heart Lake during November 16 - 19, 1965. Letters along the vertical axis identify individual animals. Each mark represents a movement across the gate at the entrance of the nest box. Note the bimodal distribution of activity between hours 17 and 22.

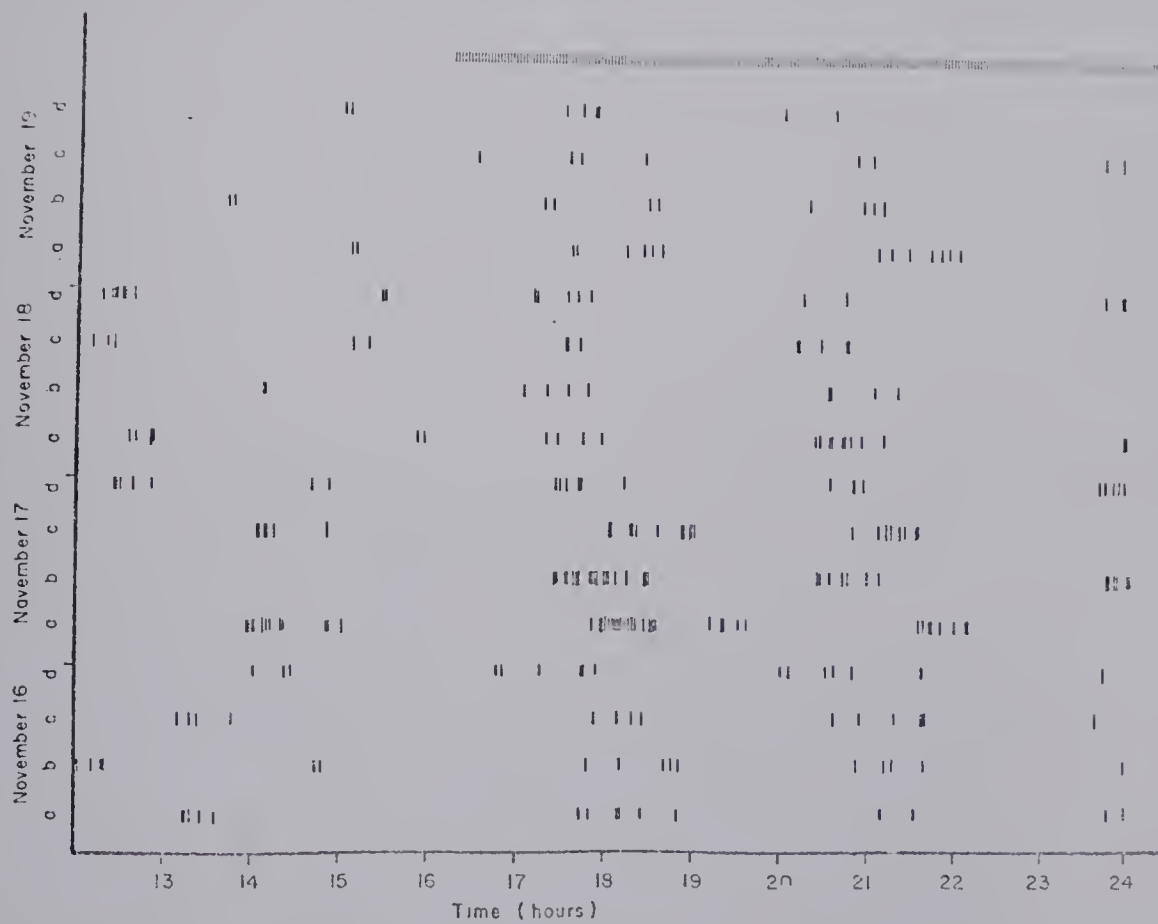
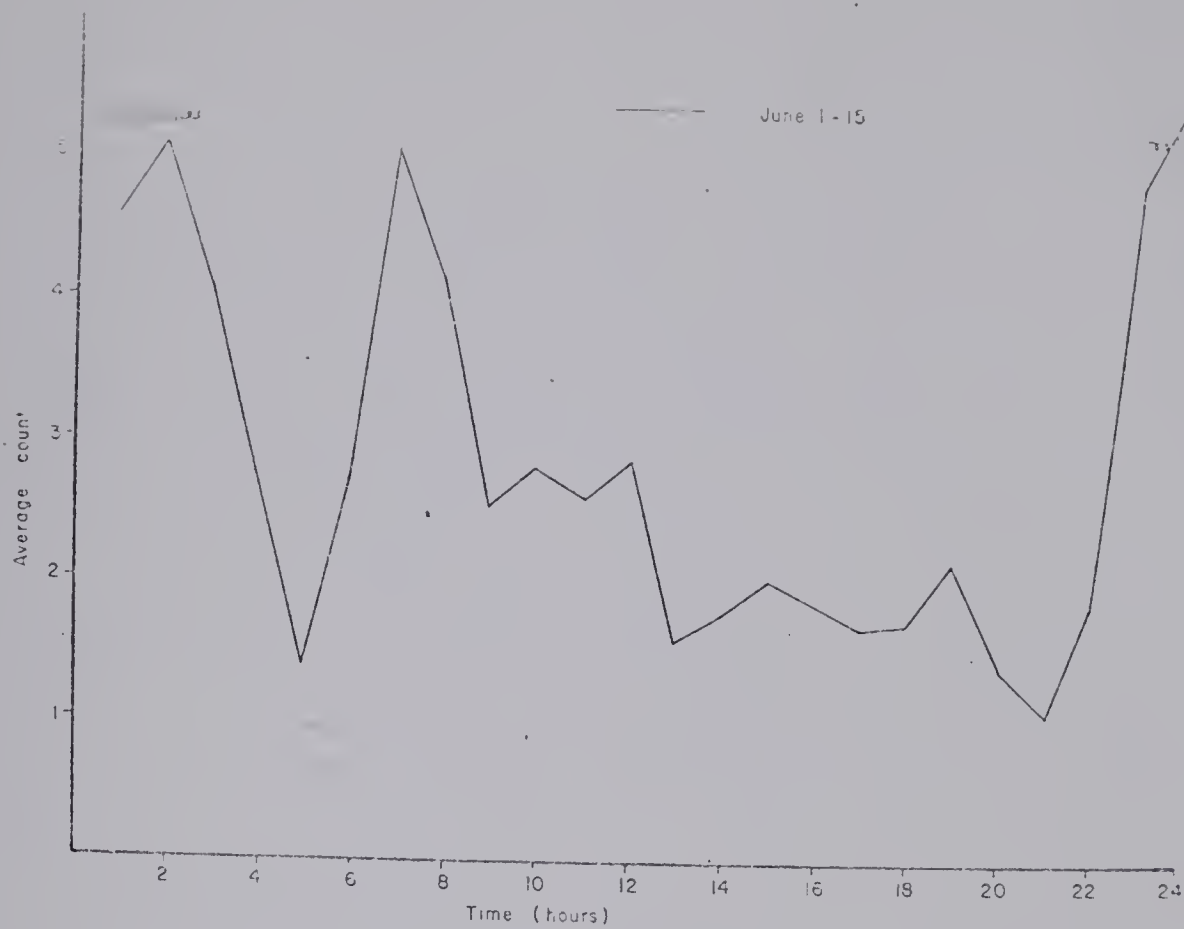


Figure 10. A transcription of raw data from activity charts of C. gapperi from Heart Lake as tested at Heart Lake during May 28 - June 1, 1966. Letters along the vertical axis identify individual animals. Each mark represents a movement across the gate at the entrance of the nest box. The distribution of activity between hour 22 and hour 8 is bimodal, a quiet period occurring between hour 4 and hour 6.

Figure 11. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during November 16 - 30, 1964. Refer to the legend for Figure 6 for details. Three males and three females, housed individually, were tested. The pattern of activity is nocturnal with a daily peak occurring after dawn.

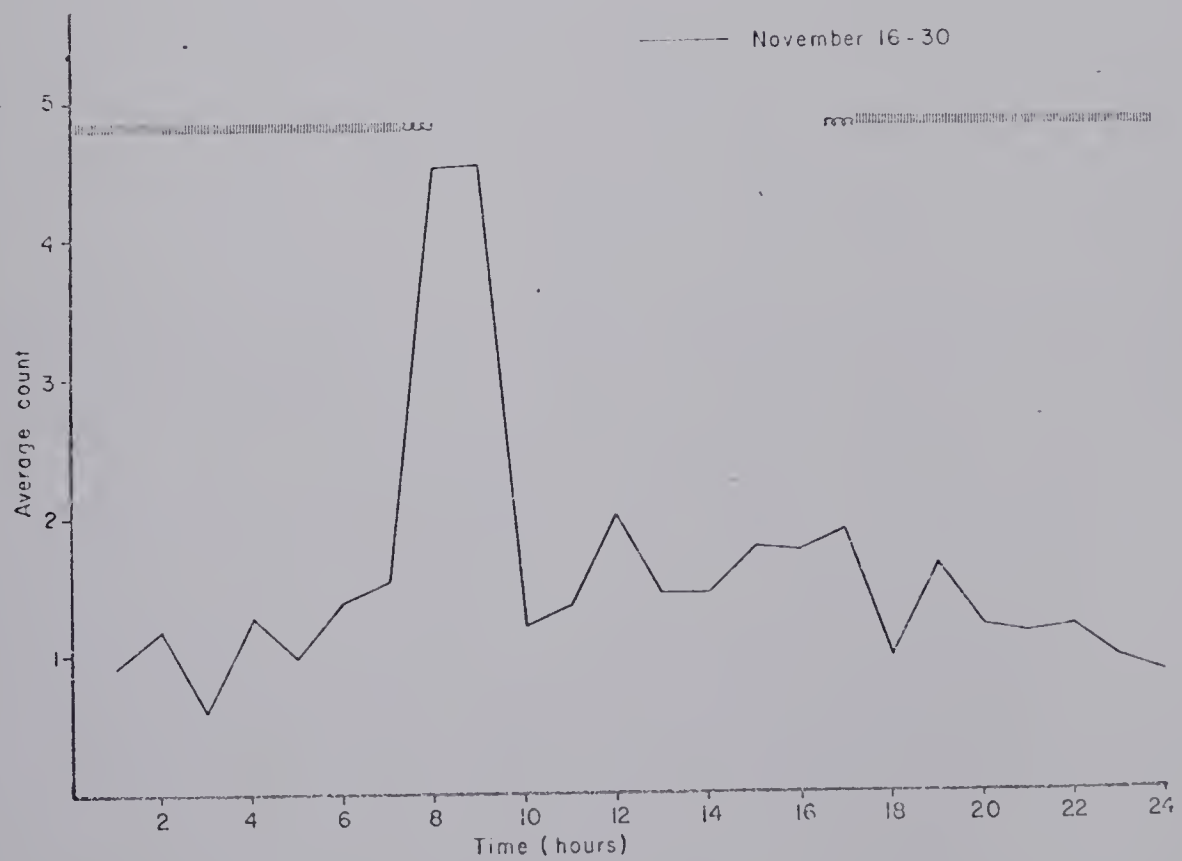
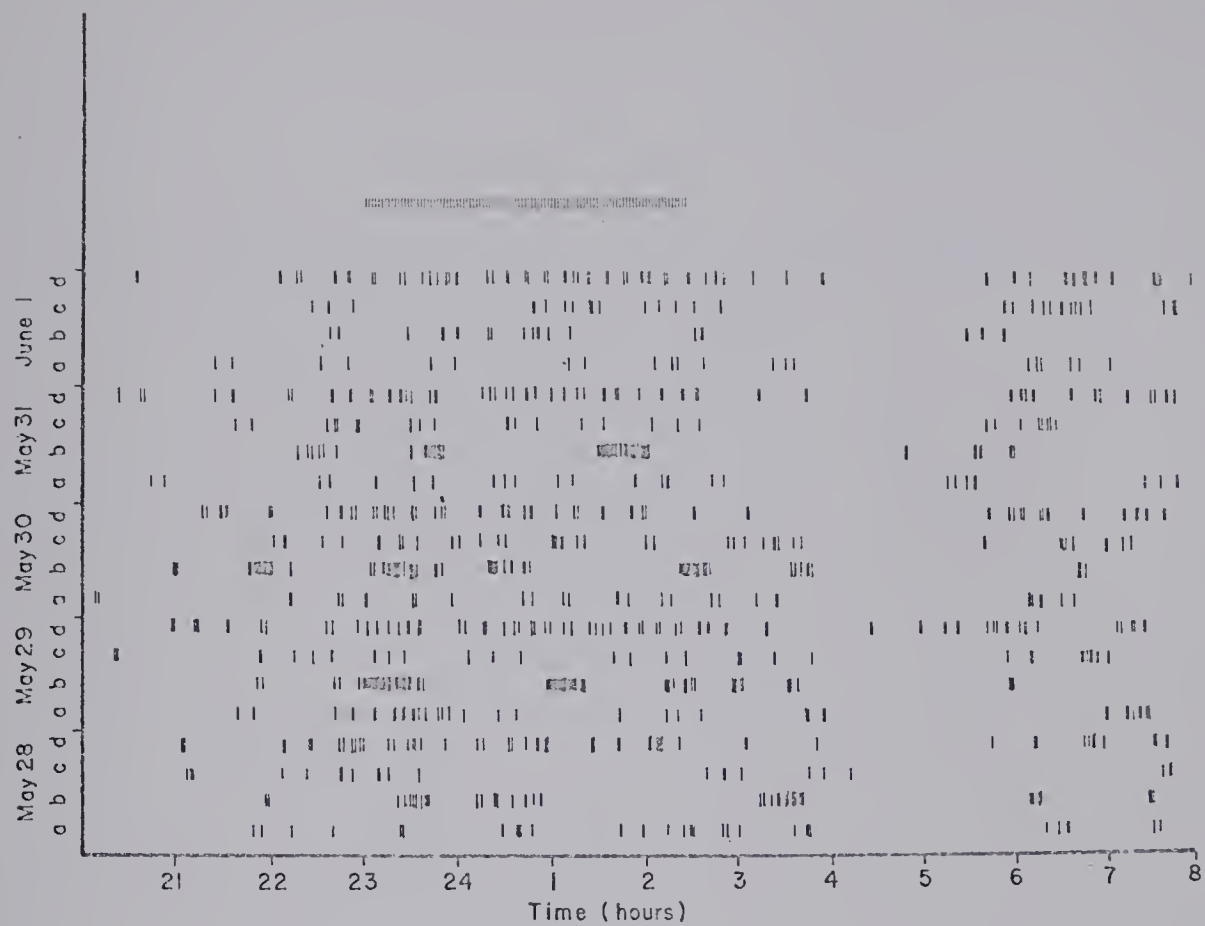


Figure 12. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during December 1 - 15 and December 16 - 31, 1964. Refer to the legend of Figure 6 for details. Three males and three females, housed individually, were tested.

Figure 13. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during January 1 - 15 and January 16 - 31, 1965. Refer to the legend for Figure 6 for details. Three males and three females, housed individually, were tested. The morning peak of activity was considerably reduced from the preceding months.

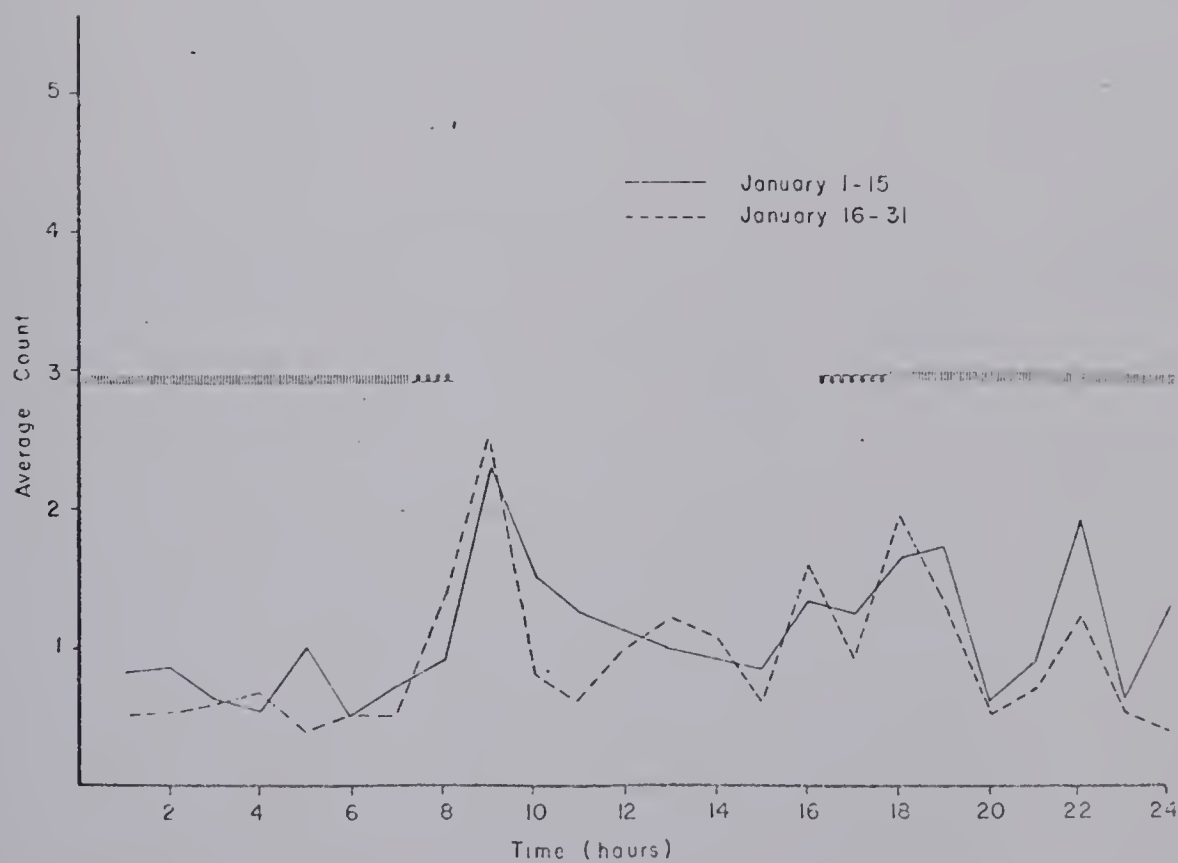
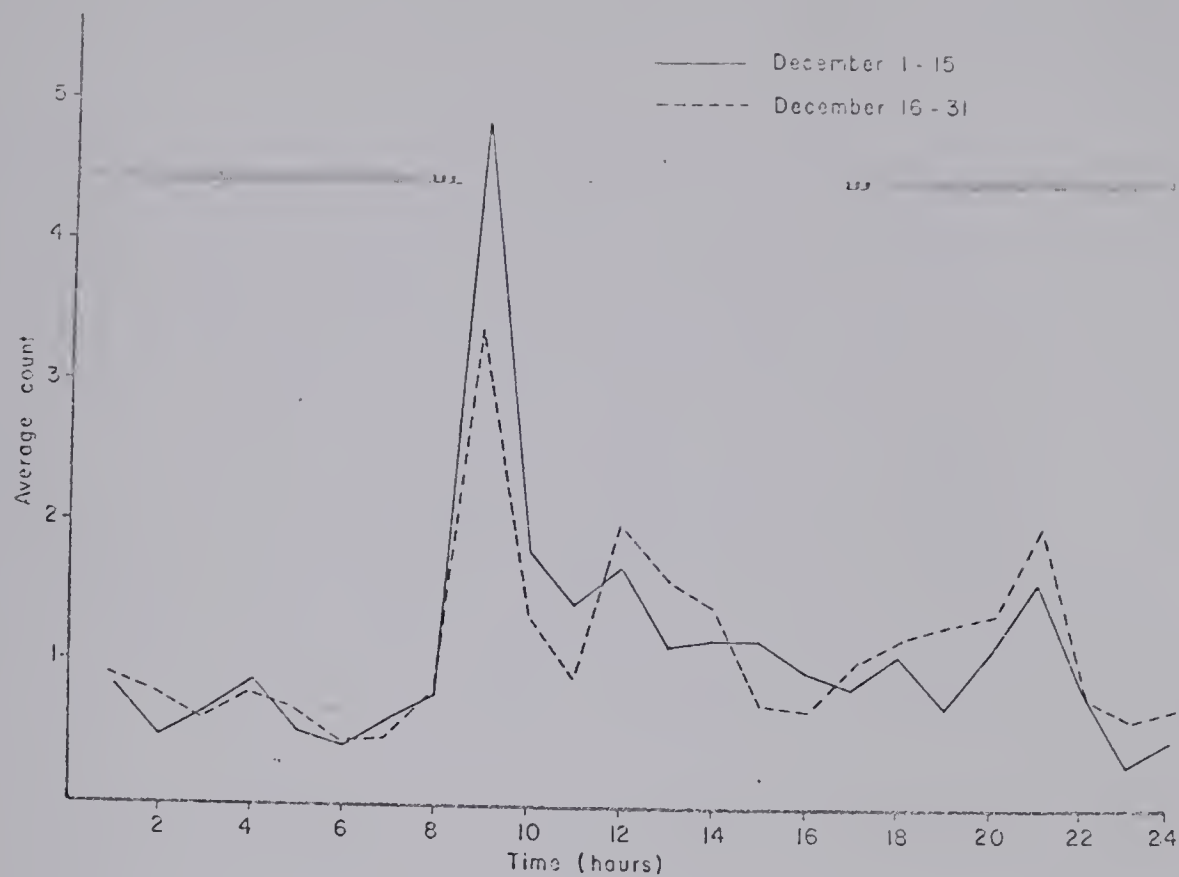


Figure 14. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during February 1 - 15 and February 16 - 28, 1965. Refer to the legend of Figure 6 for details. Three males and three females, housed individually, were tested. A typical reduced morning peak occurred in early February, but a bimodal peak occurred in the late two weeks.

Figure 15. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during March 1 - 15 and March 16 - 31, 1965. Refer to the legend of Figure 6 for details. The lower activity in late March may have been due to the colder temperatures in late than in early March. Three males and three females, housed individually, were tested.

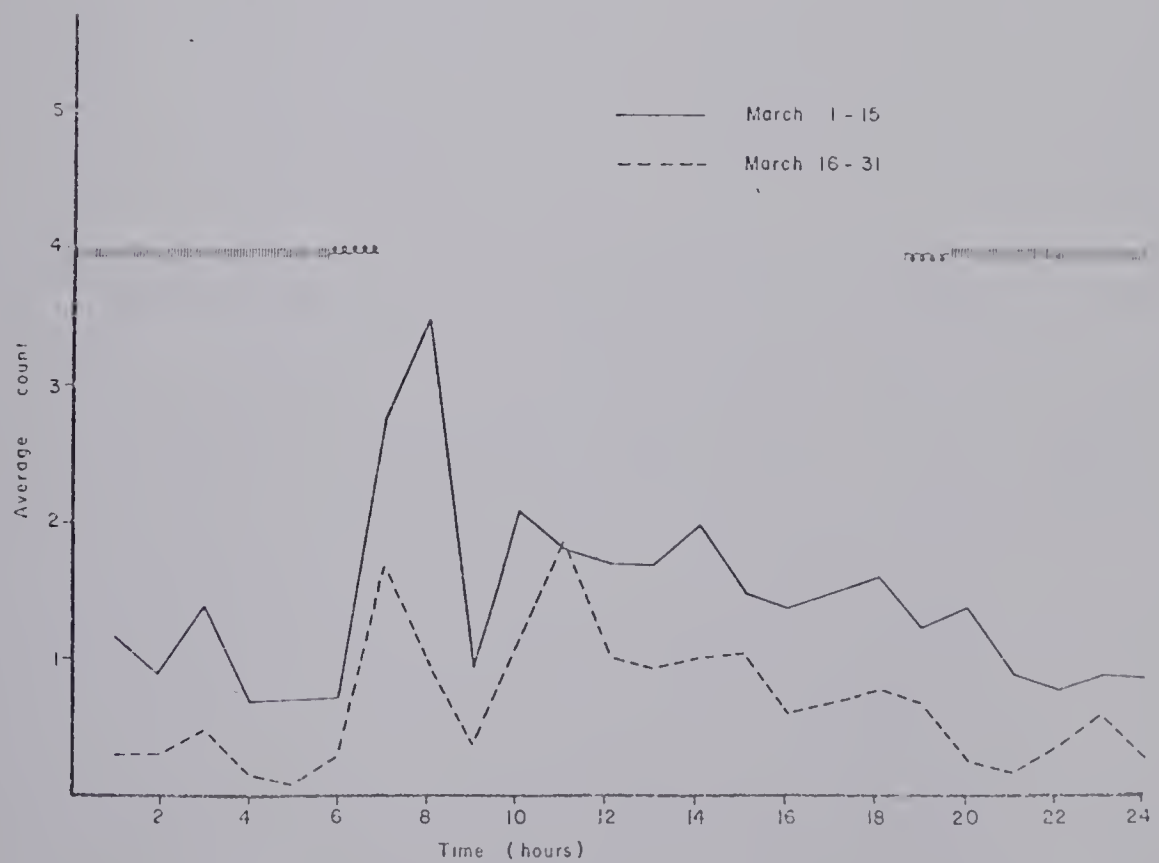
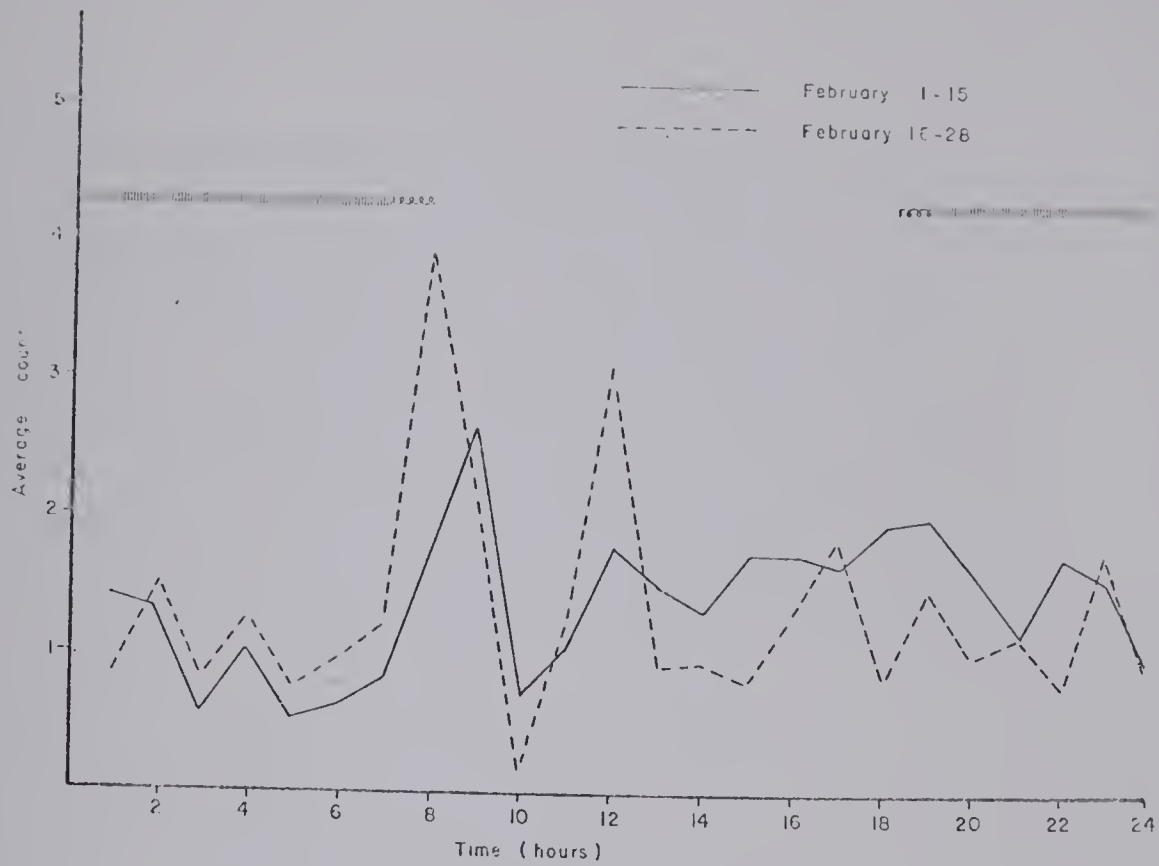


Figure 16. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton during April 1 - 15 and April 16 - 30, 1965. Refer to the legend of Figure 6 for details. Three males and three females, housed individually, were tested. The morning peak of activity increased somewhat in late April.

Figure 17. Daily activity patterns of C. gapperi from Edmonton as tested at Edmonton between May 1 and June 30, 1965. Refer to the legend of Figure 6 for details. Three males and three females, housed individually, were tested. The morning peak of activity increased in amplitude and duration from May to June. The level of non-peak activity also increased in this period.

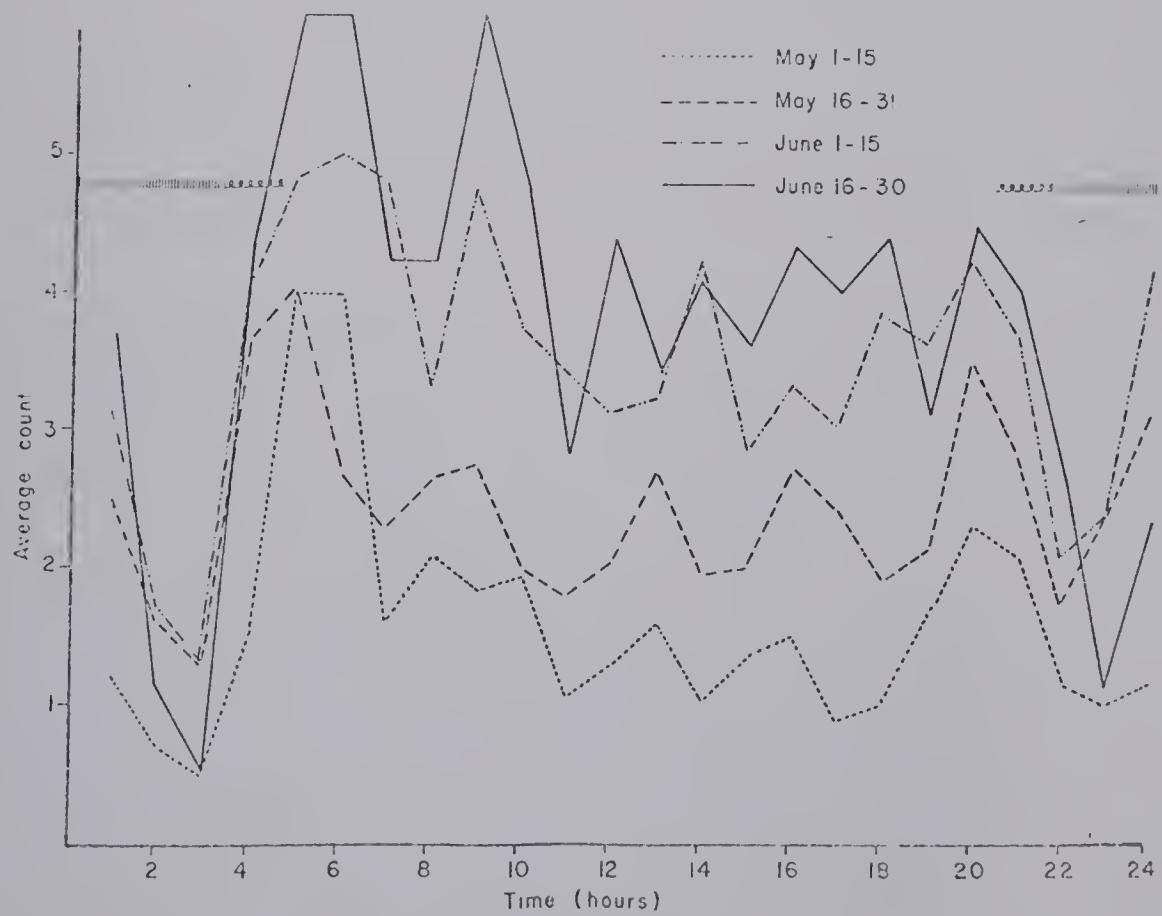
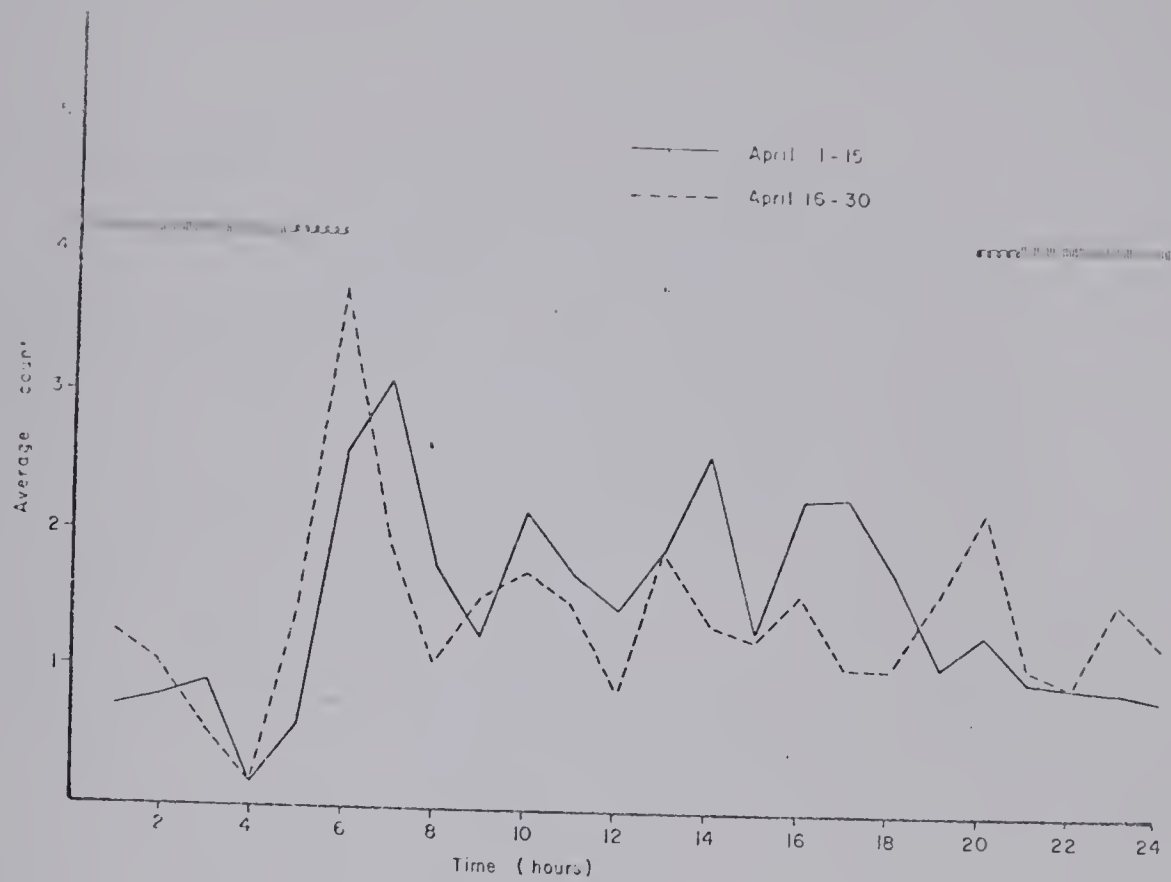


Figure 18. A transcription of raw data from activity charts of the Edmonton population of C. gapperi experiments on December 21 and 22, 1964. Letters along the vertical axis identify individual animals. Each mark represents a movement across the gate at the entrance of the nest box. Note the concentration of activity between hours 8 and 9 which corresponds to the morning peak of activity shown in Figure 16.

Figure 19. A transcription of raw data from activity charts of the Edmonton population of C. gapperi experiments on June 23 - 27, 1965. Letters along the vertical axis identify individual animals. Each mark represents a movement across the gate at the entrance of the nest box. Note that the concentrated activity between hours 3 and 12, corresponding to the morning peak of activity shown in Figure 17, consists of varying numbers of short term cycles which last from a few minutes to a few hours.

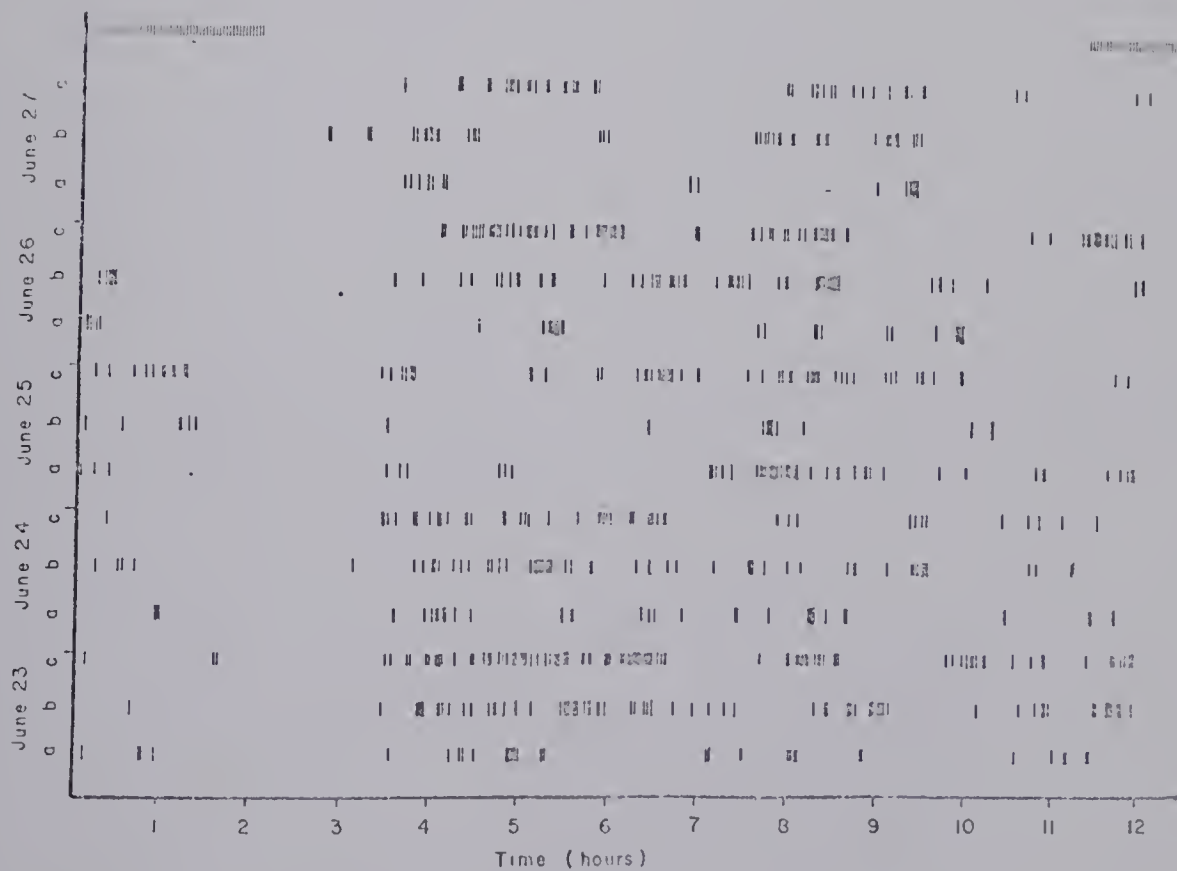
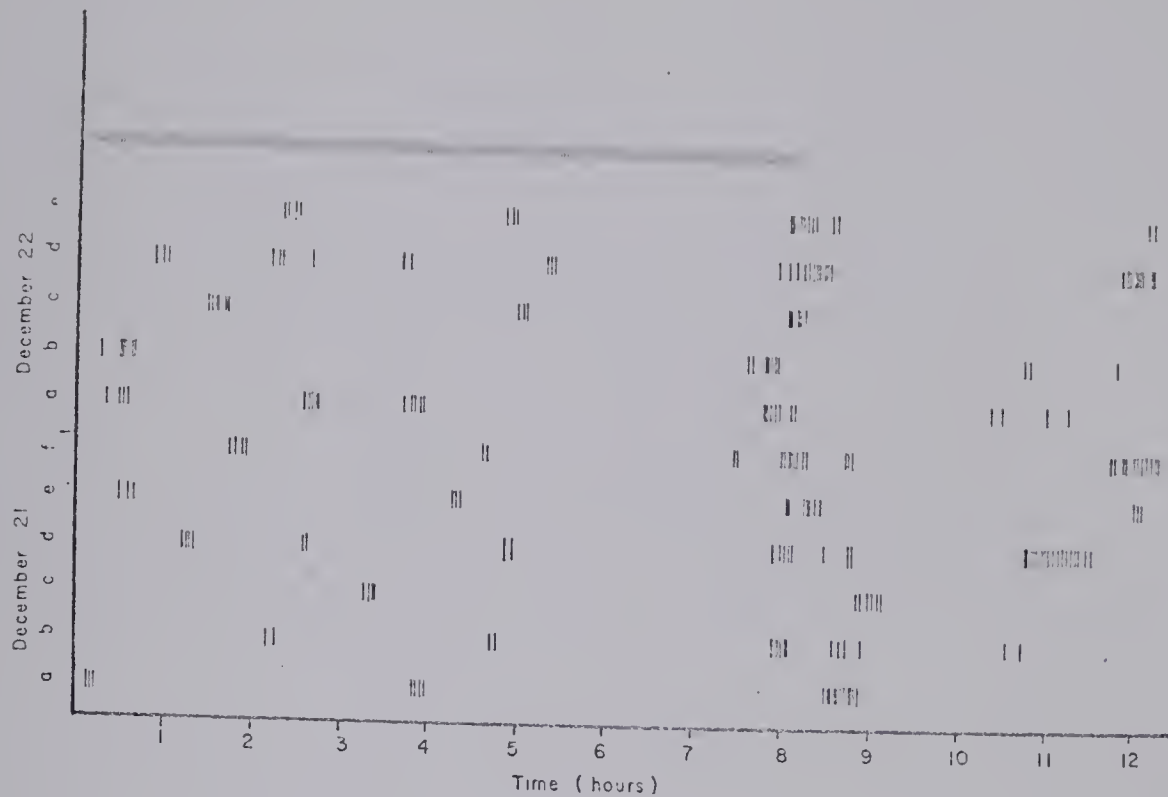


Figure 20. Daily patterns of activity of C. gapperi from Edmonton and Heart Lake as tested at Edmonton during November 16 - 30, 1964. Refer to the legend of Figure 6 for details. Three males and three females of each population were tested. Note that the Heart Lake voles, when tested at Edmonton, had similar circadian rhythms.

Figure 21. Daily patterns of activity of C. gapperi from Edmonton and Heart Lake as tested at Edmonton during December 1 - 15, 1964. Refer to the legend of Figure 6 for details. Three males and three females of each population were tested. The circadian rhythms of the two populations are similar.

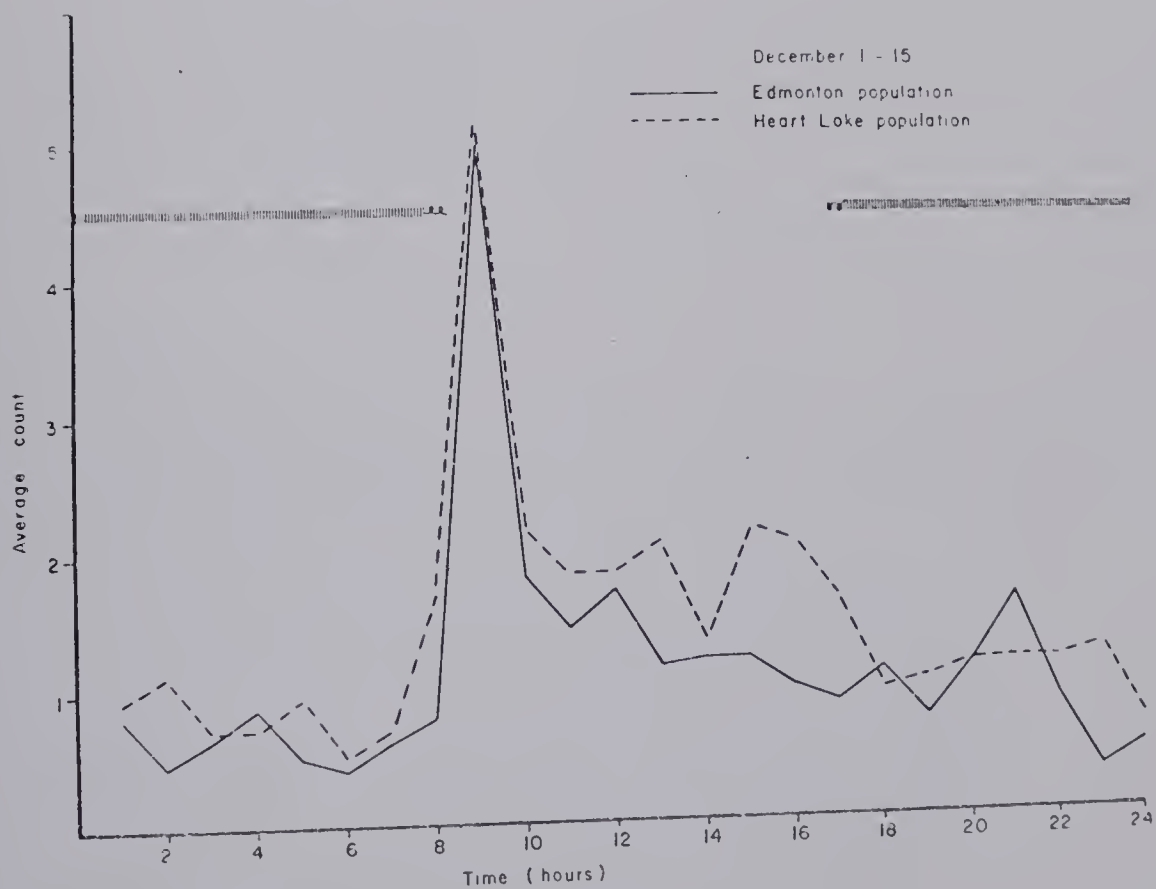
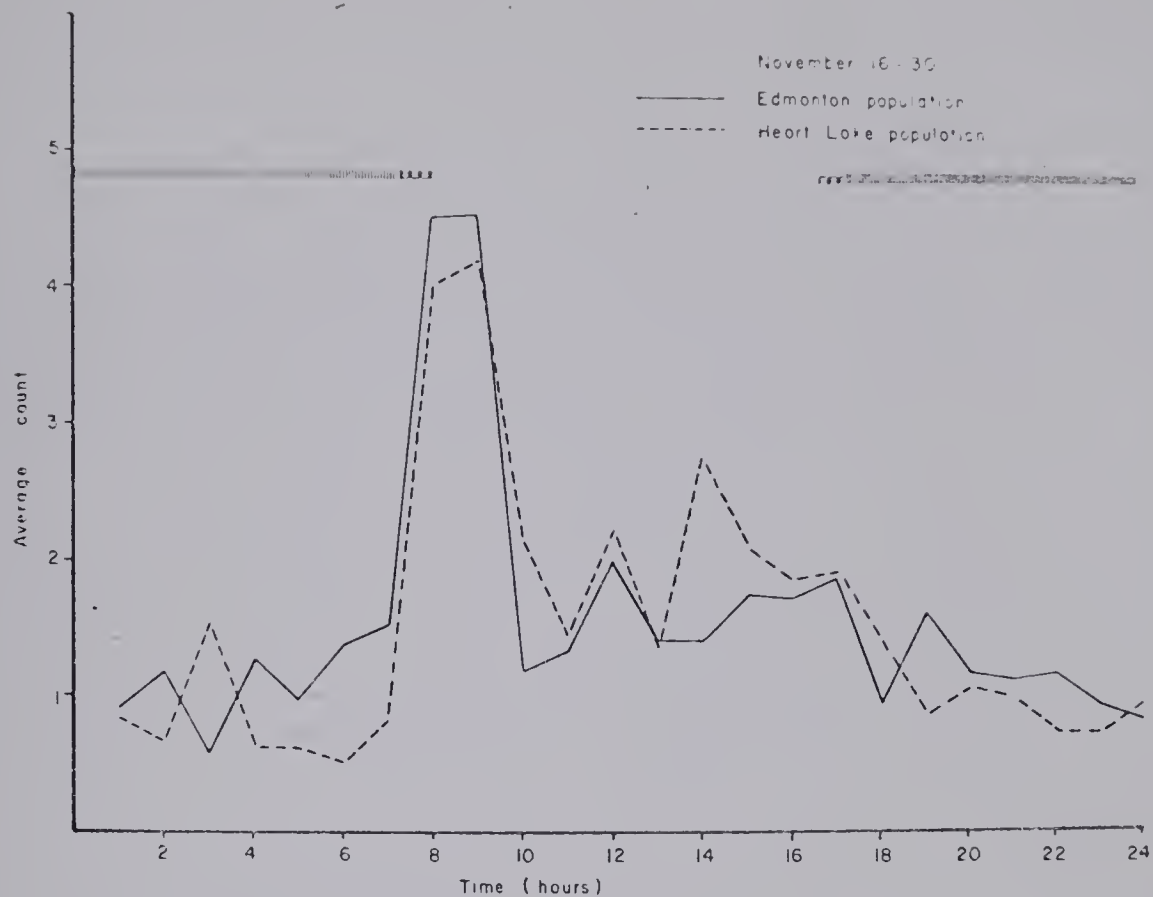


Figure 22. Daily activity patterns of C. gapperi from Edmonton and Heart Lake as tested at Edmonton during December 16 - 31, 1964. Refer to the legend of Figure 6 for details. Three males and three females of each population were tested. The morning peaks of activity of each group are reduced from the two previous test periods.

Figure 23. Daily activity patterns of C. rutilus from Heart Lake as tested at Heart Lake during November 16 - 30 and December 1 - 15, 1965. For details, refer to the legend of Figure 6. Two males and two females were tested. The pattern appears polyphasic, though a small peak may be present between hour 17 and hour 19.

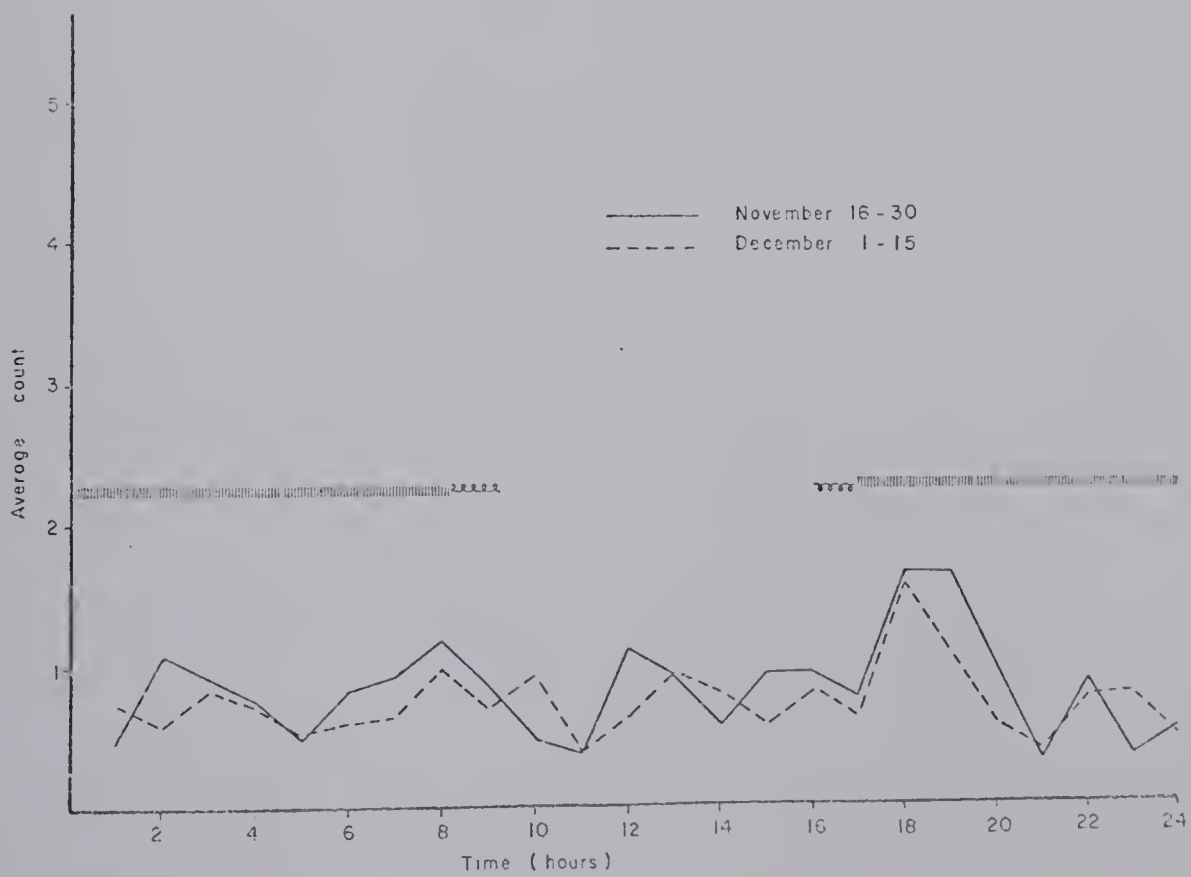
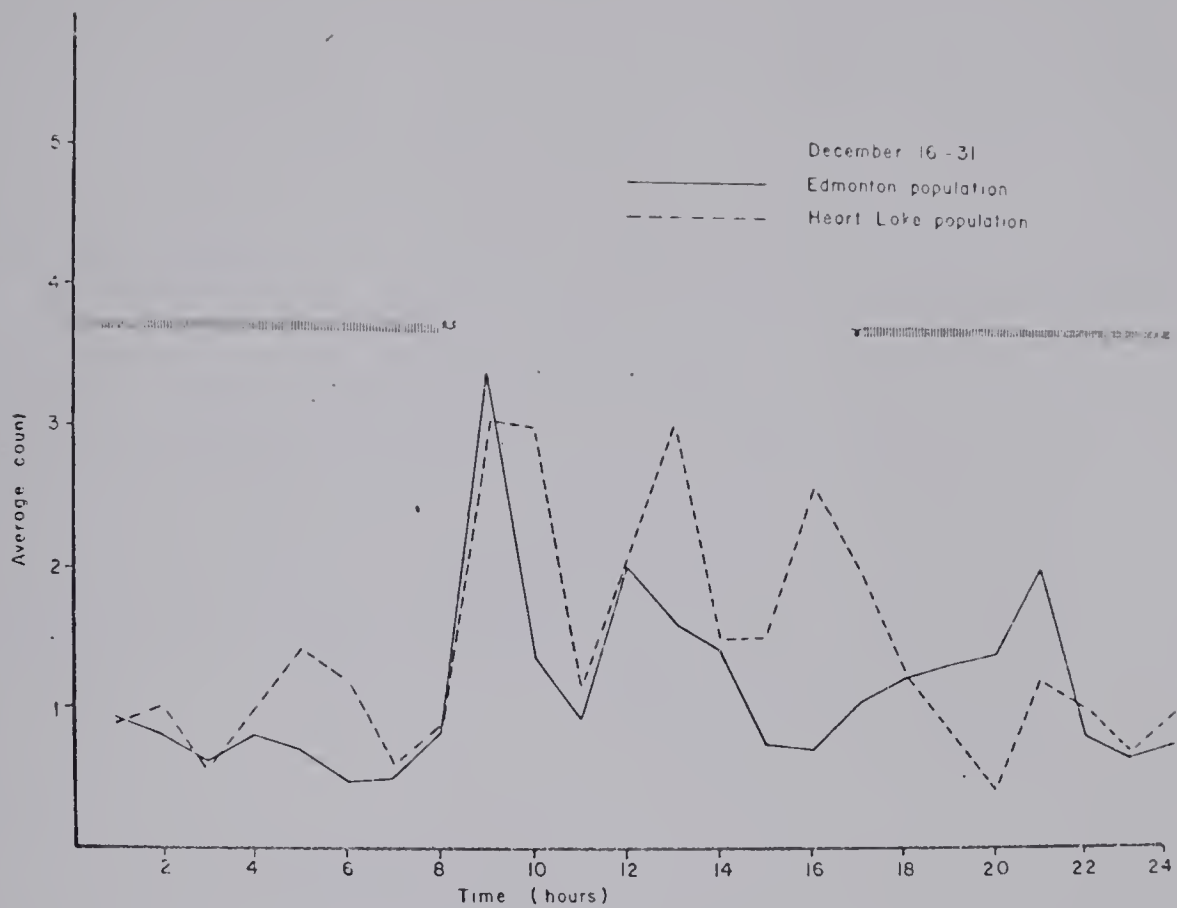


Figure 24. Daily activity patterns of C. rutilus from Heart Lake as tested at Heart Lake during May 1 - 15 and May 16 - 31, 1966. Refer to the legend of Figure 6 for details. Two males and two females were tested. The marked nocturnal peak of activity in late may was considerably reduced in early May.

Figure 25. Daily activity patterns of C. rutilus from Heart Lake as tested at Heart Lake during June 1 - 15, 1966. Refer to the legend of Figure 6 for details. Two males and two females were tested.

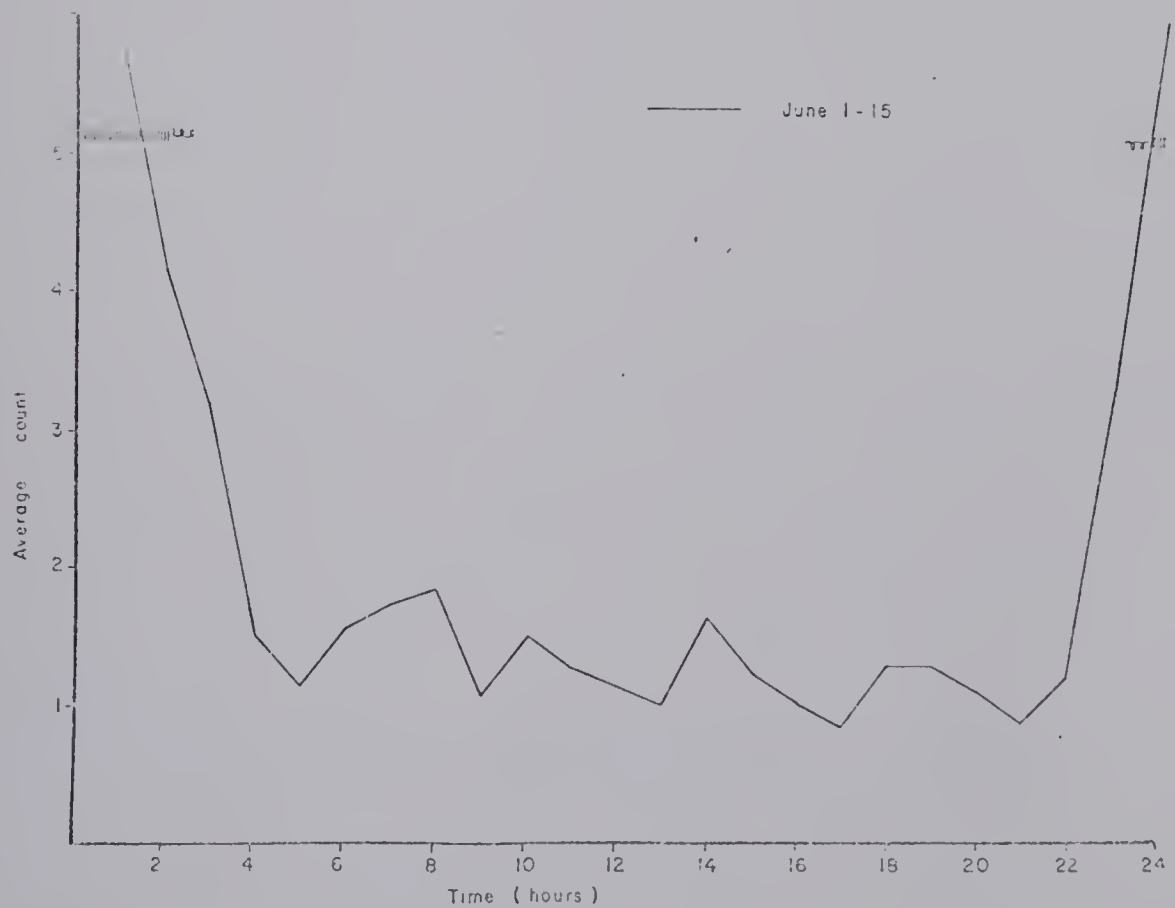
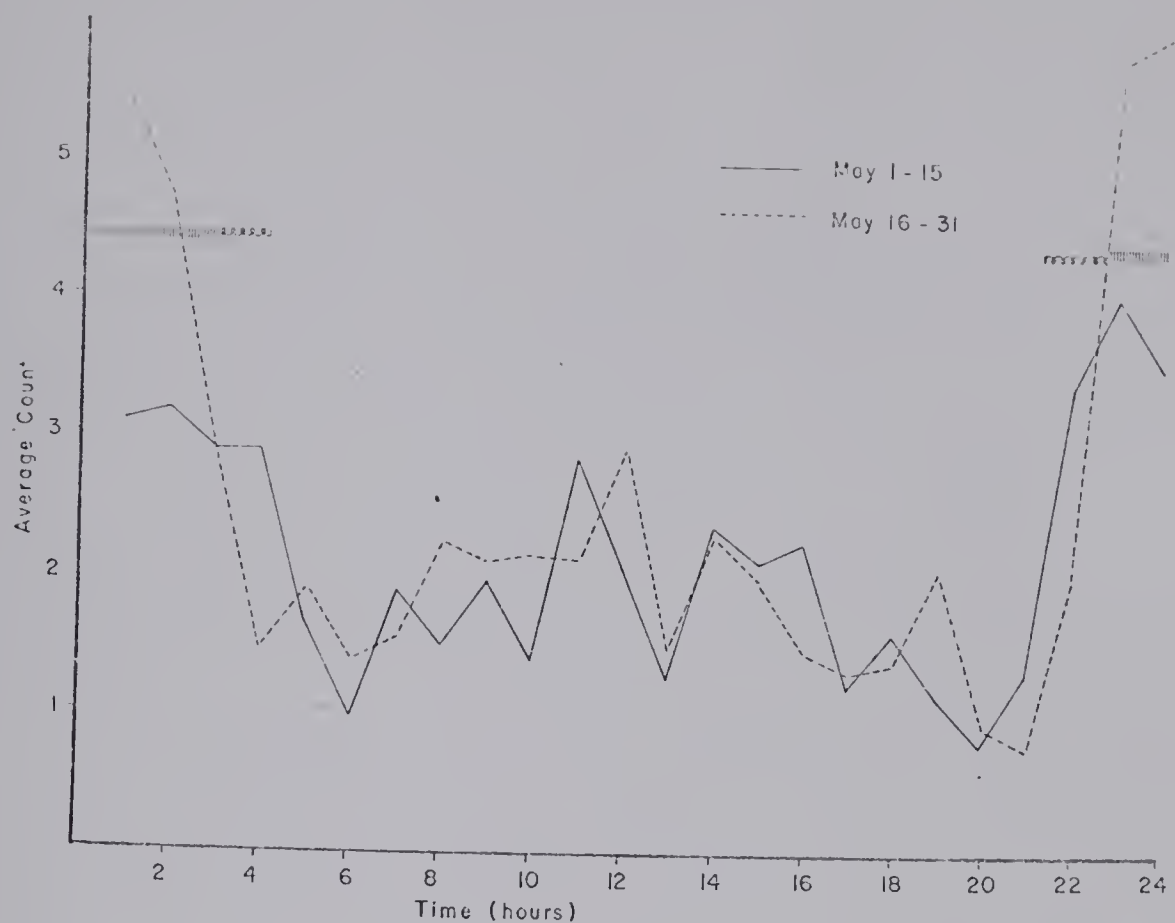


Figure 26. Daily activity patterns of P. maniculatus as tested at Heart Lake during November 16 - 30, December 1 - 15 and December 16 - 31, 1965. Refer to the legend of Figure 6 for details. Two males and one female, housed in a single nest box, were tested. It should be noted that the level of activity was higher in the dark than in the light hours.

Figure 27. Daily activity patterns of P. maniculatus as tested at Heart Lake during January 1 - 11, 1966. Refer to the legend of Figure 6 for details. Two males and one female, housed in a single nest box were tested. The activity was considerably reduced by torpor during this period.

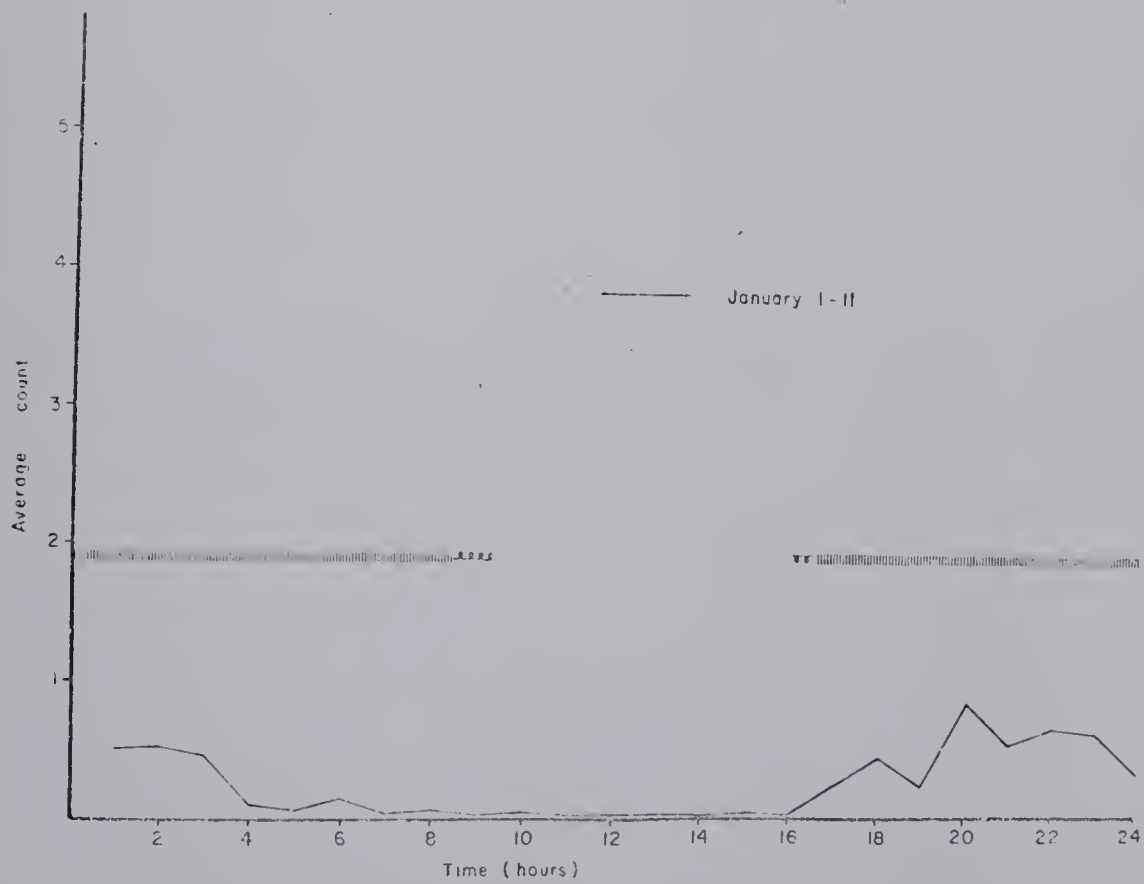
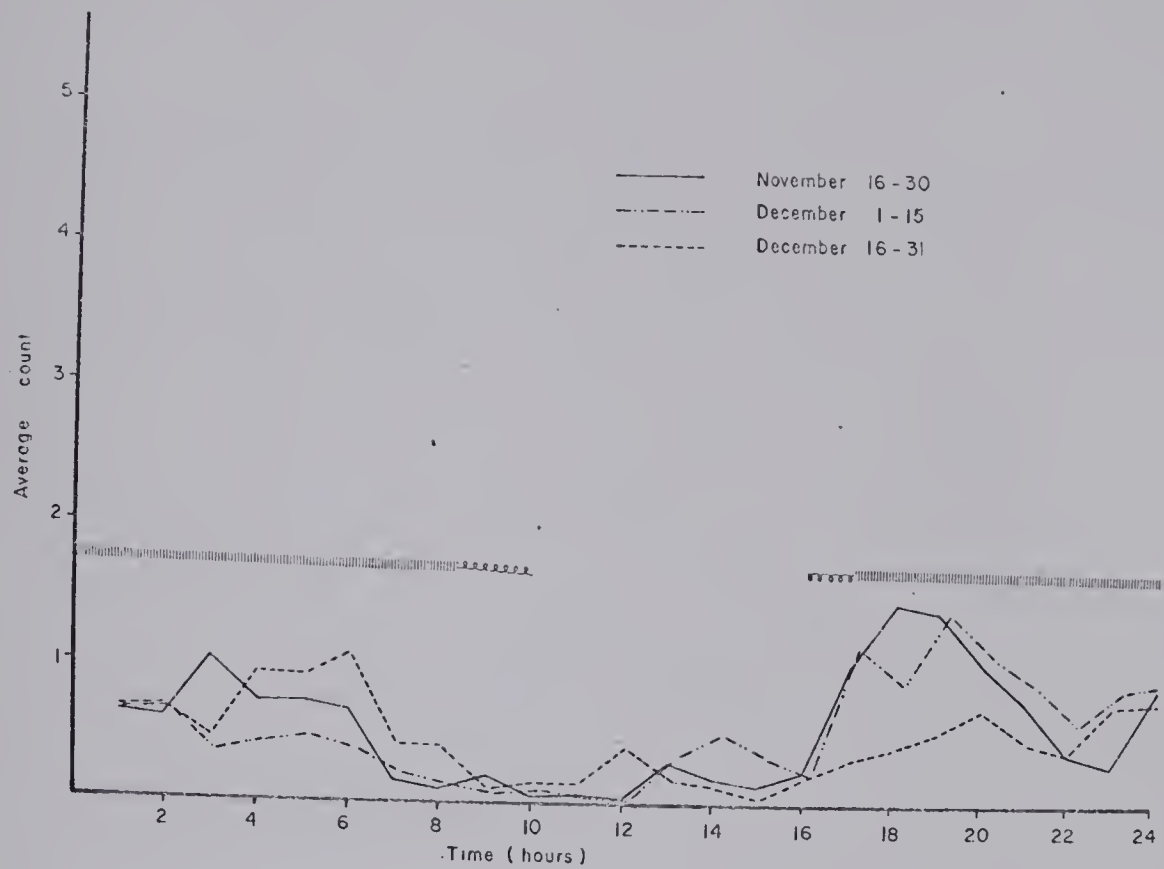


Figure 28. Daily activity patterns of P. maniculatus as tested at Heart Lake during March 1 - 8, March 19 - 31 and April 1 - 15, 1966. Refer to the legend of Figure 6 for details. Two males and one female were tested. They were housed in a single nest box during March 1 through 8. They were housed individually in late March and early April. The level of activity increased and a definite, nocturnal circadian rhythm developed as the temperature warmed and the mice came out of torpor in late March and early April.

Figure 29. Daily activity patterns of P. maniculatus as tested at Heart Lake during April 16 - 30 and May 1 - 15, 1966. Refer to the legend of Figure 6 for details. Two males and one female, housed individually, were tested. Note that the duration of the daily peak of activity rhythm does not change as the length of the dark period shortens. Instead the animals remain active in the dusk of early evening, and the bright daylight of the first few hours of morning.

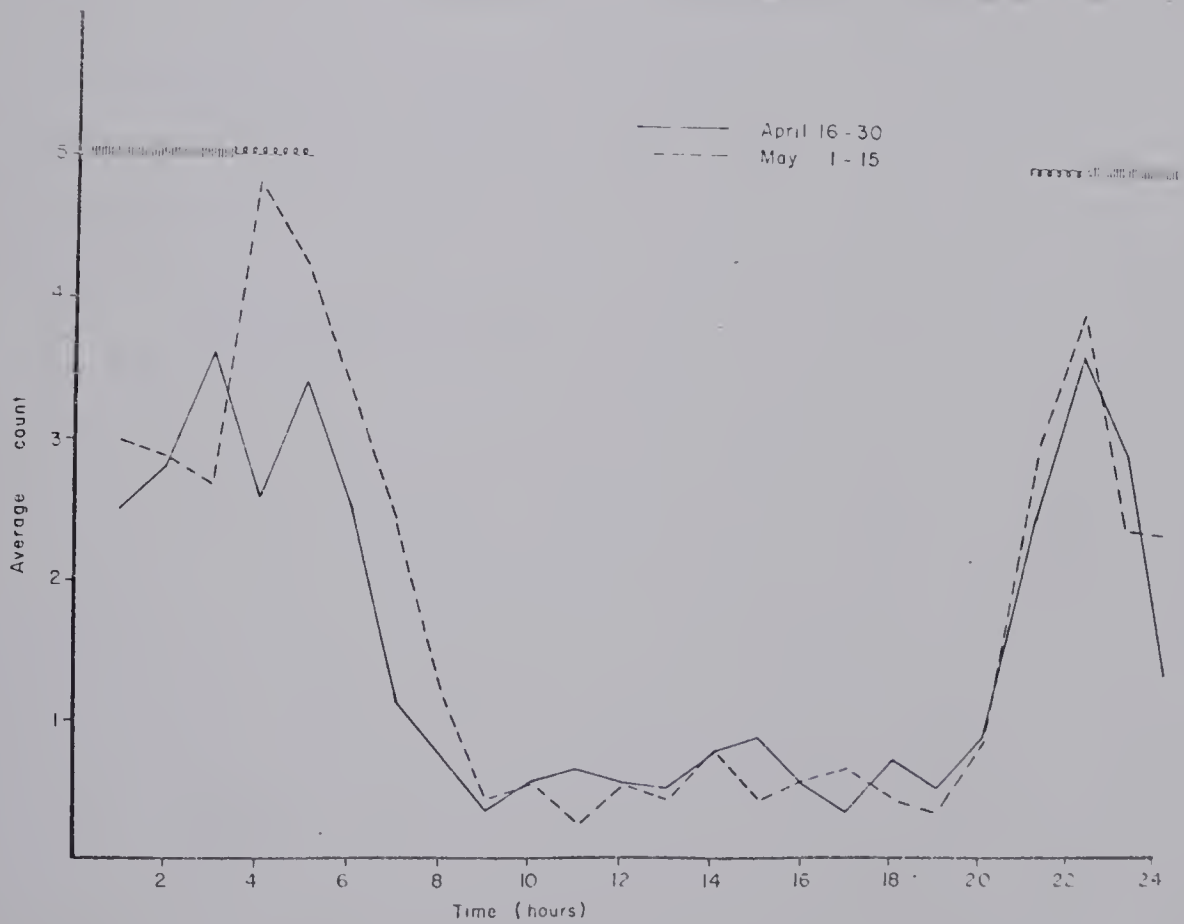
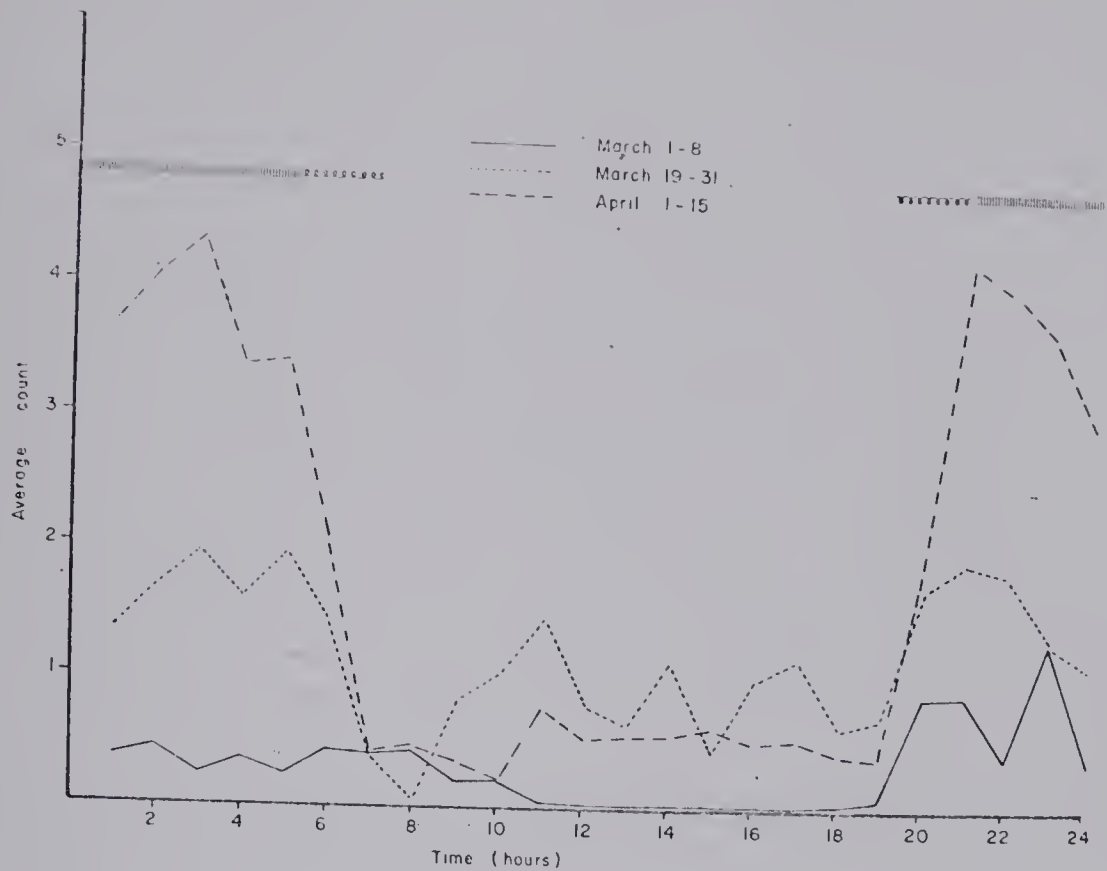
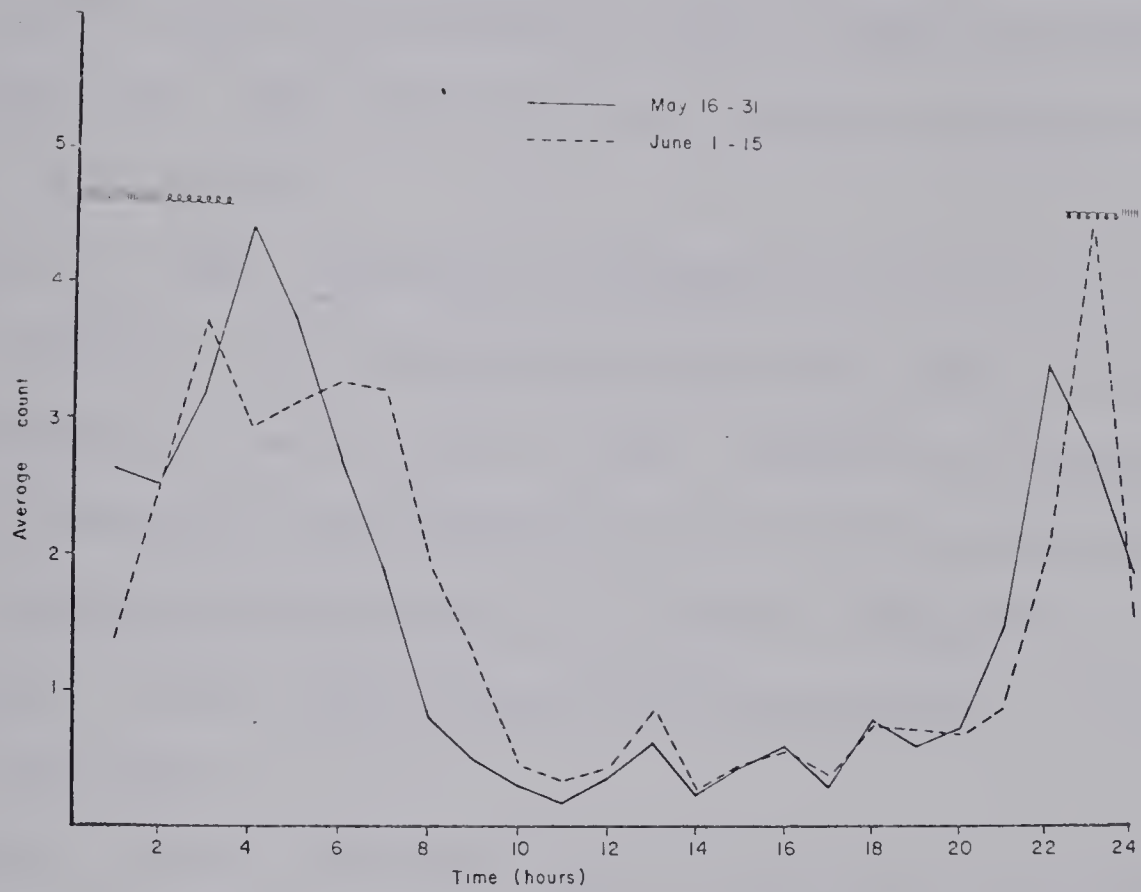


Figure 30. Daily activity patterns of P. maniculatus as tested at Heart Lake during May 16 - 31 and June 1 - 15, 1966.

Daily activity patterns of P. maniculatus as tested at Heart Lake during May 16 - 31 and June 1 - 15, 1966.

Refer to the legend of Figure 6 for details. Two males and one female, housed individually, were tested. Again, note the extension of the daily peak of activity into the first few hours of morning daylight.



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